WOOD ANATOMY OF SYMPETALOUS DICOTYLEDON FAMILIES: A SUMMARY, WITH COMMENTS ON SYSTEMATIC RELATIONSHIPS AND EVOLUTION OF THE WOODY HABIT[1]

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ABSTRACT

Data on wood anatomy are presented in tabular form for 56 sympetalous families of dicotyledons arranged according to the system of Dahlgren, who was influenced by data from presence or absence of iridoids and by embryological information. Each order is reviewed in terms of the degree of correlation of wood data with data from chemistry and embryology. Original data are presented for Buddlejaceae, Globulariaceae, and Selaginaceae. Ericales prove to be a natural and rather primitive group. Cornales as a whole are primitive, but Adoxaceae and Stylidiaceae have distinctively specialized woods. Dipsacales are highly diverse on the basis of woods, creating interpretational questions. Gentianales are a natural group on the basis of wood and of intraxylary phloem in primary stems; Oleales and Rubiales are peripheral to Gentianales. Scrophulariales and Lamiales have specialized wood and are probably natural groupings, but there is no difference between the orders on the basis of wood anatomy. Recognition of particular families within Scrophulariales and Lamiales is aided by wood anatomy: Buddlejaceae, Globulariaceae, and Selaginaceae are distinctive families in Scrophulariales; Avicenniaceae, Chloanthaceae, and Stilbaceae (the last of which should include Retziaceae) should be recognized in Lamiales. Wood anatomy does not aid in differentiating Solanales from Boraginales. Wood of Asterales is rather uniform in characters of major evolutionary significance, despite its diversity in ecological wood anatomy. Lamiales and Scrophulariales have wood similar to that of Asteraceae, but so do Apiaceae, which share chemical features with Asteraceae, Campanulales, and some Dipsacales. Among families *incertae sedis*, Desfontainiaceae (often relegated to Loganiaceae) should be recognized under Cornales near Escalloniaceae, as should Columelliaceae. Fouquieriaceae bear resemblances to Cornales and Ericales, but deserve isolation in a monofamilial order. Familial assignment of the genera *Leucophyllum*, *Oftia*, and *Paulownia* is discussed.

During the past three decades, numerous studies on wood anatomy of sympetalous families have been published; prior to this, these kinds of studies were relatively few. The majority of sympetalous families are predominantly herbaceous, and in the first half of the twentieth century, most wood studies dealt with predominantly woody families. This bias was based upon the origin of wood studies in forestry programs. As wood anatomy entered botany, a broader view developed. Data on wood anatomy suitable for comparison of the sympetalous dicotyledon families are now available, so that a comparison of wood data with other information is timely.

Although I have monographed wood of many sympetalous families, I have not done original re-search on some, notably Apocynaceae, Bignoniaceae, Rubiaceae, and Verbenaceae. Various workers have contributed data for these families, and the patterns revealed are relatively clear and form a good basis for conclusions about the systematic distribution of wood features.

The predominantly herbaceous nature of several of the sympetalous families is significant, in that wood anatomy in these predominantly herbaceous groups differs from that in typically woody families. Paedomorphosis in secondary xylem (Carlquist, 1962a) is a concept based largely on study of sympetalous families. Paedomorphosis is not encountered in typically woody plants, yet in families such as Plantaginaceae, wood of all species exhibits this phenomenon. Small shrubs of limited duration

also exhibit a form of this phenomenon (Carlquist, 1989). The occurrence of paedomorphic features in wood is valuable in showing shifts in habit: for example, the raylessness of *Calceolaria* is indicative that the shrubby species of the genus have been derived from herbaceous ancestors. Other paedomorphic features also indicate change in habit, which is discussed in a concluding section of this paper.

Another inherent interest in the wood of sympetalous families is the sensitive way in which wood features reflect ecology. The earliest papers in my survey of wood anatomy of Asteraceae (Carlquist, 1957a, 1958a, 1959) revealed a close relationship between the habitat of a species and its wood anatomy, particularly with respect to vessel features, and a summary paper on Asteraceae (Carlquist, 1966b) profiled the nature of these trends. Subsequent studies on sympetalous dicotyledon families have confirmed and expanded these findings. To be sure, some families of dicotyledons do not cover wide ecological latitude and are characteristic of wet habitats only (e.g., Aquifoliaceae, Cornaceae, Lauraceae). The sympetalous families are unusual within dicotyledons in the degree to which they have entered dry and hot habitats, and thus they show ecological wood anatomy exceptionally well. Ecological wood anatomy is not a focus of the present paper, but is mentioned because features of ecological significance must be separated from those that indicate relationship.

One can point to ecology as the cause for progression not merely in quantitative vessel features, but in major trends as well (e.g., alteration of the perforation plate from scalariform to simple). Because the major trends have developed in a coordinated way (e.g., ray histology has changed concomitantly with vessel specialization), the specialized end products have virtually no possibility of appreciable or wholesale reversion. The features reported as sensitive to local ecology are mostly easily reversible. Asteraceae are virtually uniform with respect to the "major trends of xylem evolution" (storying is absent in the majority of the family and only occurs in a few species). However, vessel features in Asteraceae vary greatly with respect to ecology.

This example shows that if other sympetalous families follow the pattern of Asteraceae, they are excellent for documenting ecological wood anatomy. The Asteraceae, Convolvulaceae, Lamiaceae, and Scrophulariaceae show trends in ecological wood anatomy very well.

Not all wood features of these and other sympetalous families vary with respect to local ecology.

There is a residue of wood features distributed according to taxonomic groupings. Wood features have perhaps been thought too often to be decisive in systematic matters—and in a few cases, they are. For the most part, however, wood anatomy is of help to various degrees in various parts of the taxonomic system. Wood anatomy can be used to identify a wood specimen in many cases, so obviously there are wood features that correspond to the taxonomic system. However, wood features tend to be most useful for identification at the generic level, somewhat less at the familial level, and least at the ordinal level. If this generalization is true, it indicates that wood anatomy could aid phylogenetic studies such as this survey of the sympetalous families. Identification of woods has been stressed by such features as inclusion in texts of keys to genera based on wood anatomy; however, it is not as useful as such keys would indicate. Keys and computer programs utilizing wood features of the major genera of economic importance have been presented. If the wood anatomy of large numbers of the world's woody species were added to these presentations, one would find that many species could not be distinguished from one another. I can underline this by saying that if I were handed samples belonging to Scrophulariaceae, Solanaceae, or Lamiaceae, I could not say with certainty, on the basis of wood anatomy, that they were not from species of Asteraceae.

Nevertheless, wood anatomy does show distinctive distribution of features with respect to the taxonomic system. For example, successive cambia occur in Avicenniaceae and Chloanthaceae, but not in Verbenaceae sensu stricto. Thus, occurrence of successive cambia offers reinforcement for segregation of Avicenniaceae and Chloanthaceae (Carlquist, 1981a). Another verbenoid group, Stilbaceae, merits segregation on the basis of wood anatomy (Carlquist, 1986). Two families often assigned to Scrophulariaceae, Globulariaceae and Selaginaceae, are distinctive on the basis of wood anatomy (see below).

Particular distinctive genera may prove to be misplaced according to wood data. In the present study, Buddlejaceae prove not to belong near Loganiaceae, but close to or within Scrophulariales. This agrees with results of other studies presented in this volume. Evidence will be presented for familial reassignment of *Leucophyllum* and *Oftia* (often placed in Myoporaceae) as well. On the basis of wood anatomy, *Retzia*, a monotypic South African genus sometimes placed in its own family, can be assigned to Stilbaceae. The assignment of *Paulownia* (often regarded as intermediate be-

tween Bignoniaceae and Scrophulariaceae) is not simplified by data from wood anatomy.

Evolutionary level of wood features is not a reliable indicator of relationships: discrepancies can occur between related families. If families all share essentially the same level of advancement in wood features, the concordance tends to be regarded as a confirmation of relationship. However, gaps in evolutionary level of wood between families claimed to be related on other groups do not negate relationship. They must, presumably, be explained eventually. In the sympetalous families of Dipsacales, Caprifoliaceae have primitive wood, Dipsacaceae somewhat more specialized wood and the Calyceraceae and Valerianaceae highly specialized wood. Various explanations for these divergent levels of wood advancement may be suggested. However, as Bailey (1944) stressed, we cannot envision phylads with primitive wood being derived from those with specialized wood. Thus, Calyceraceae and Valerianaceae cannot be ancestral to Dipsacaceae and Caprifoliaceae. Levels of wood evolution may be regarded as ways of negating relationship even though they cannot decisively confirm relationship. Where wood features of a series of families agree (e.g., banded apotracheal axial parenchyma in Gentianales), similar wood levels (all of these have tracheids or tracheidlike fiber-tracheids) may be regarded as subsidiary evidence of relationship. As stated above, wood rarely gives strong evidence for ordinal groupings. In the present review, Gentianales are the only order in which wood evidence may be an aid to ordinal delimitation.

Because evidence from wood may often be confirmatory though not decisive, comparison with results from other approaches is valuable. In fact, the evidence from wood anatomy does not contradict the evidence and cladograms presented in the other studies presented in this volume. Notable in this regard is the tendency for groups with specialized woods to appear in terminal branches of the clades proposed, whereas those with primitive wood occupy more basal positions. Primitive woods in Ericales can be cited as an example.

The orders and families of sympetalous dicotyledons are discussed here according to the sequence of the Dahlgren (1975) system. A few exceptions to this system have been incorporated, however. Donoghue et al. (1992) show that *Sambucus* (in Sambucaceae of Cornales according to the Dahlgren system) belongs in Dipsacales and is closely related to *Adoxa*, which they place in Adoxaceae rather than Caprifoliaceae. They place *Sambucus* in Adoxaceae (older as a familial name than

Sambucaceae) and include Adoxaceae in Dipsacales. That treatment is followed here. Although the accompanying papers give evidence for placement of Goodeniaceae in the clade leading to Asteraceae, the noncommittal placement of Goodeniaceae in Goodeniales, following Dipsacales, has been retained here.

Comments on various systems of classification for the sympetalous families are not offered in the present paper. The paper by Wagenitz (1992) summarizes the various schemes of classification as they related to the sympetalous families of dicotyledons.

Data Available

Table 1 summarizes data on iridoid presence, wood features, and selected embryological features. The data in Table 1 on iridoids are based on Jensen et al. (1975) and Dahlgren et al. (1976, 1979). Dahlgren's (1975) classification scheme, which has (with a few exceptions) been followed here, was influenced by patterns of iridoid occurrence. Dahlgren (1975) included choripetalous families within some orders in which sympetalous families occur. All choripetalous families have been omitted from Table 1, with the exception of Apiaceae, which are included in the terminal section of the table among families of uncertain position. Apiaceae have been included as an example of a choripetalous family that might be related to some sympetalous families, such as Asteraceae. Araliaceae, mentioned by Dahlgren (1975) as possibly related to sympetalous dicotyledons, have not been included because the closely related Apiaceae are slightly more specialized with respect to wood features and thus show more similarities to the sympetalous families. Apiaceae have some chemical characters characteristic of Asteraceae: presence of polyacetylenes and sesquiterpene lactones (Hegnauer, 1971). The other families relegated to the end of Table 1 are those in which systematic position either has been controversial (Fouquieriaceae), or in which the systematic position proves to be less clear than previously thought when wood data, along with other kinds of information, are assessed (Desfontainiaceae, Salvadoraceae). The systematic position of some families in the main part of Table 1 is not clear, however (for example, the position of Stylidiaceae). The majority of authors in the present volume who comment on familial interrelationships agree that Buddlejaceae belong in Scrophulariales; that finding, confirmed by wood data, is incorporated in Table 1. Some segregate families are recognized here (Duckeodendraceae, Goetzeaceae, and

TABLE 1. Chemical, xylary, and embryological features of sympetalous dicotyledons.

Order	Family	1 IRI	2 PER	3 HEL	4 VES	5 ITE	6 VAS
Ericales	Cyrillaceae	?	C	0	0	T	0
	Ericaceae	1, 4	C, i	(+)	(+)	T	+
	Epacridaceae	?	C	(+)	0	T	0
Cornales	Columelliaceae	?	C	0	0	T	0
	Alseuosmiaceae	?	C	0	0	L	0
	Stylidiaceae	1	I	0	0	F	0
Loasales	Loasaceae	4	c, I	0	0	T	0
Dipsacales	Caprifoliaceae	6, 7, 10	C	0	0	T	0
	Adoxaceae	6, 10	I	0	0	L	0
	Dipsacaceae	6, 7	I	0	0	T	0
	Valerianaceae	6, 10	c, I	0	0	L	0
	Calyceraceae	6	I	0	0	L	0
Goodeniales	Goodeniaceae	6, 7, 10	I	0	0	T	0
Gentianales	Loganiaceae	6, 7, 9, 10	I	(+)	+	F, T	+
	Gentianaceae	6, 7, 10	I	0	0	T	0
	Apocynaceae	1, 6, 7, 9, 10	c, I	(+)	+	F, T	(+)
	Asclepiadaceae	?	I	0	+	F, T	+
	Rubiaceae	1, 2, 9, 10	c, I	(+)	+	F, T	0
Oleales	Oleaceae	4, 6, 10	I	+	(+)	F, T	+
Scrophulariales	Buddlejaceae	1	I	+	0	L	+
	Scrophulariaceae	1, 2, 10	c, I	+	0	F, L	0
	Globulariaceae	1	I	0	0	T	0
	Selaginaceae	10	I	+	0	F, L	+
	Plantaginaceae	1, 10	I	0	0	L	0
	Pedaliaceae	2	I	0	0	L	0
	Marytniaceae	1	I	0	0	L	0
	Gesneriaceae	?	c, I	0	0	F	0
	Bignoniaceae	1, 10	c, I	(+)	0	L	0
	Myoporaceae	1, 10	I	0	0	F	0
	Acanthaceae	10	I	0	0	L	+
Lamiales	Verbenaceae	1, 2, 3, 4, 10	c, I	+	(+)	L	+
	Lamiaceae	1, 2, 10	I	+	0	L	+
	Avicenniaceae	?	I	0	0	L	0
	Chloanthaceae	?	I	0	0	F	0
	Stilbaceae	10	c, I	0	0	F	+
Plumbaginales	Plumbaginaceae	0	I	+	0	L	+
Ebenales	Ebenaceae	0	I	0	0	F	0
Primulales	Primulaceae	0	I	0	0	L	0
	Myrsinaceae	0	I	0	0	L	0
	Theophrastaceae	0	I	0	0	L	0
Asterales	Asteraceae	0	I	+	0	L	+
Campanulales	Pentaphragmataceae	?	C	0	0	F	0
	Campanulaceae	0	c, I	0	0	L	0
	Lobeliaceae	0	I	0	0	L	0
Solanales	Solanaceae	0	I	+	0	F, T	+
	Goetzeaceae	?	I	0	0	F	+
	Duckeodendraceae	?	I	0	0	F	0
	Nolanaceae	?	I	0	0	F	0
	Convolvulaceae	0	I	0	0	F	0
	Polemoniaceae	0	I	0	0	F, L	0
Boraginales	Hydrophyllaceae	0	I	0	0	F	+
	Boraginaceae	0	I	+	+	F	0
Incertae Sedis	Apiaceae	0	I	0	0	L	0
	Desfontainiaceae	?	C	0	0	T	0
	Fouquieriaceae	1, 2, 3, 4	I	0	0	T	?
	Salvadoraceae	?	I	0	0	L	

Explanation of abbreviations. Column 1 (IRI) = presence of iridoids (types, if present, according to the system of Jensen et al., 1975); Column 2 (PER), perforation plate (I = simple, S = scalariform); Column 3 (HEL) = presence or absence of helical thickenings in vessels; Column 4 (VES) = presence or absence of vesturing in vessels; Column 5 (ITE) = imperforate tracheary elements (F = fiber-tracheids, L = libriform fibers, T = tracheids); Column 6 (VAS) = vasicentric tracheids present or absent; Column 7 (RAY) = ray types (E = heterogeneous, L = rayless, O = homogeneous, P = paedomorphic, numerical types according to the schemes of Kribs, 1935, and Carlquist, 1988a); Column 8 (AXP) = axial parenchyma (Ab = abaxial, Al = aliform, B = apotracheal banded, C = confluent, D = diffuse, DA = diffuse in aggregates, 0 = absent, S = scanty vasicentric, V = abundant vasicentric); Column 9 (STO) = storying present or absent; Column 10 (PAE) = paedomorphic features of wood (L = rayless, R = rays, S = occasional scalariform perforation plates); Column 11 (VAR) = cambial variants (I = interxylary phloem, 0 = normal, S = successive cambia); Column 12 (INT) = integuments (B = bitegmic, U = unitegmic); Column 13 (NUC) = nucellus (Cr = crassinucellate, T = tenuinucellate); Column 14 (END) = endosperm (C = ab initio cellular, H = helobial, N = nuclear). Lower case letters indicate character state is restricted to only one or two genera.

TABLE 1. Continued.

7 RAY	8 AXP	9 STO	10 PAE	11 VAR	12 INT	13 NUC	14 END
E2A, E2B	D	0	0	0	U	T	N
E1, E2A, E3	D, Ab	0	0	0	U	T	N
E2A	D	0	0	0	U	T	N
E3	D, S	0	0	0	?	?	?
E1, L	D	0	L	0	?	?	?
L	0	+	L	I, U	U	T	C
E2A, L, P1	D	+	C, L, R	0	U	T	C
E1, E2A	D, s	0	0	0	U	T	C
E2B	S, T	+	0	0	U	T	C
E2A	D, S	0	0	0	U	T	C
P1, P2	S	+	C, R	0	U	T	C
P1	S	0	R	0	U	T	C
E2B, P1	Ab, D, T	0	R	0	U	T	C
E2A, E3, O1	B, S, T	0	0	I	U	T	N
P1	S	+	R	I	U	T	N
E1, E2A, E3	Ab, DA, S, T	+	0	0	U	T	N
E2B, P1	D, DA, S	0	R	0	U	T	N
E1, E2A, E3, P1	B, D, S	(+)	R	s	U	T	c, N
E1, E2, E2, O1, O2	Al, C, d, S	0	0	0	U	T	C
E2B	Ab, D, S	0	0	0	U	T	C
E1, E2A, E2B, L, P1	S, 0	+	L, R	0	U	T	C
E2B	D, S	0	0	0	U	T	C
L	0	0	L	0	U	T	C
L	0	+	L	0	U	T	C
E2B, P1	S	+	R	0	U	T	C
E2B, P1	S	0	R	0	U	T	C
E2B, P1	S, 0	+	L, R	0	U	T	C
E2	A, Al, C, S	+	0	0	U	T	C
E2B, O1	S	+	0	0	U	T	C
E2B, L, P1	S	0	L, R	I	U	T	C, h
E2A, E2B, O2	Al, C, S, V	+	r	0	U	T	C
E2A, E2B	S, V	0	r	0	U	T	C
O1	D, S, V	0	0	S	U	T	C
E2B, P1	S	0	R	S	U	T	C
E2B, P1	S	0	R	0	U	T	C
E2B, P1	S	0	R	S	B	Cr	N
E2, E3, O1	B, V	+	0	0	B	T	C
L	D	0	L	0	B	T	N
E2B, O2	S	0	0	0	B	T	N
E2B, O2	0, S	0	0	0	U	T	N
E2B, L, P1	S	+	L, R	s	U	T	C, N
L	0	0	L, R, S	0	U	T	C
P1	S	0	R, S, V	0	U	T	C
P1, P2	S	0	R, V	0	U	T	C
E2B, E3, O1, O3, P1	B, D, DA, 0, S	0	R	0	U	T	C
E2B, O1	D, DA	0	0	0	U	?	?
O1	B, V	0	0	0	U	?	?
E2B, P1	B, S	0	0	0	U	T	C, h
E2B, P1, P3	Al, B, D, S	0	R	S	U	Cr, T	N
E2B, L, P1	B, S	0	L, R	0	U	T	N
E2B, L, P1	D, 0	0	L, R	0	U	T	N
E2B, O2, P1	A1, C, D, DA	+	R	0	U	T	C, N
E2, P1	S, T	0	R	0	U	T	N
E3	D	0	0	0	?	?	?
O1	D	0	0	0	B	T	C
E2B	D	0	0	0	B	T	C
	C, S	+	0	I	B	Cr	N

Nolanaceae in Solanales), although other authors may not employ these usages.

Data on wood anatomy in Table 1 are based upon the sources listed below; the atlas of Schweingruber (1990) contains useful data also:

Acanthaceae: Carlquist & Zona (1988). Adoxaceae (Sambucaceae): Greguss (1959). Alseuosmiaceae: Dickison (1986). Apiaceae: Metcalfe & Chalk (1950), Rodriguez (1957), and original data. Apocynaceae: Ingle & Dadswell (1953), Metcalfe & Chalk (1950). Asclepiadaceae: Metcalfe & Chalk (1950) and original data. Asteraceae: Carlquist (1957a, b, 1958a, b, 1959, 1960a, b, 1961, 1962b, 1963, 1965a, b, 1966a, b, 1982a, 1983a, b), Carlquist & Eckhart (1982). Avicenniaceae: Meylan & Butterfield (1978), Metcalfe & Chalk

(1950). Bignoniaceae: Pfeiffer (1926), Metcalfe & Chalk (1950). Boraginaceae (including Ehretiaceae): Barajas Morales (1981), Carlquist (1970b), Gottwald (1983), Nair & Mohan Ram (1989). Buddlejaceae: Mennega (1980) and present paper (see below). Calyceraceae: Carlquist (1983b). Campanulaceae: Shulkina & Zikov (1980). Caprifoliaceae: Ogata (1988), Metcalfe & Chalk (1950). Columelliaceae: Stern et al. (1969). Convolvulaceae: Mennega (1969), Pant & Bhatnagar (1975), Lowell & Lucansky (1986), Carlquist & Hanson (1991). Cyrillaceae: Thomas (1960) and original data. Desfontainiaceae: Mennega (1980). Dipsacaceae: Carlquist (1982b). Duckeodendraceae: Carlquist (1988b). Ebenaceae: Metcalfe & Chalk (1950). Epacridaceae: Meylan & Butterfield (1978), Metcalfe & Chalk (1950). Ericaceae: Metcalfe & Chalk (1950), Carlquist (1985). Fouquieriaceae: Henrickson (1986), Carlquist & Hoekman (1985), and original data. Gentianaceae: Carlquist (1984b). Gesneriaceae: Carlquist & Hoekman (1986a). Globulariaceae: present paper (see below). Goetzeaceae: Carlquist (1988b). Goodeniaceae: Carlquist (1969b). Hydrophyllaceae: Carlquist et al. (1983), Carlquist & Eckhart (1984). Lamiaceae: Rudall (1981), Carlquist (1992). Loasaceae: Carlquist (1984c, 1987c). Lobeliaceae: Carlquist (1969a). Loganiaceae: Mennega (1980), Coulaud (1988). Martyniaceae: Carlquist (1987b). Myoporaceae: Carlquist & Hoekman (1986b). Myrsinaceae: Metcalfe & Chalk (1950), Meylan & Butterfield (1978). Nolanaceae: Carlquist (1987a). Oleaceae: Parameswaran & Vidal Gomes (1981), Baas et al. (1988). Pedaliaceae: Outer & Veenendal (1983), Carlquist (1987b). Pentaphragmataceae: Carlquist (1975) and original data. Plantaginaceae: Carlquist (1970a). Plumbaginaceae: Metcalfe & Chalk (1950) and original data. Polemoniaceae: Carlquist et al. (1984). Primulaceae: original data. Rubiaceae: Koek-Noorman (1969a, b, 1970, 1972, 1976), Koek-Noorman & Puff (1983), Welle et al. (1983). Salvadoraceae: Outer & Veenendal (1981). Scrophulariaceae: Cristiani (1945), Michener (1981, 1983, 1986). Selaginaceae: present paper (see below). Solanaceae: Carlquist (1991). Stilbaceae (including Retziaceae): Carlquist (1986). Stylidiaceae: Carlquist (1981b). Theophrastaceae: Metcalfe & Chalk (1950). Valerianaceae: Carlquist (1983b). Verbenaceae: Metcalfe & Chalk (1950).

References that report only a few features for one or two species in a family (e.g., reports of vesturing in vessels) are not included in the above listing. Data on embryology of the sympetalous

families are from Davis (1966) and Kapil & Vijayaraghavan (1965).

MATERIALS AND METHODS

Original data are presented below for one species of Globulariaceae and for two species of Selaginaceae. In addition, original data are presented for several Buddlejaceae as part of a review of that family. Woods of these families were available in dried form. The methods employed in study of these families are the same as those described in my recent papers.

For sympetalous dicotyledons as a whole, wood terminology generally follows that of the IAWA Committee on Nomenclature (1964). Exceptions occur in the cambial variants, for which the terminology follows Carlquist (1988a).

NEW DATA

When contemplating the present paper, I had not intended to report on species belonging to Globulariaceae and Selaginaceae (both families are included in Scrophulariaceae by some authors). However, these segregate families proved to have distinctive wood anatomy, the details of which had not been described before. I collected wood of both families, so that presentation of documented data was possible. There is no information on wood of Globulariaceae or Selaginaceae in Metcalfe & Chalk (1950). This is probably related to the limited size of shrubs in these families, which consist mostly of herbaceous plants. *Globularia salicina* Lam. is exceptional in having stems up to ca. 1 cm diam.; its shrubby habit may be related to occupancy of frost-free localities in the Canary Islands. Selaginaceae form shrubs smaller than that, and stems never attain 1 cm diam., to the best of my knowledge.

GLOBULARIACEAE

Globularia salicina Lam., *Carlquist 2629* (RSA), Tenerife, Canary Islands (Figs. 35–38). Growth rings inconspicuous (Fig. 35). Vessels mostly solitary (Fig. 35), mean number of vessels per group, 1.23. Vessels rounded in transection (Fig. 36). Mean vessel lumen diameter at widest point, 14 μm. Mean number of vessels per mm^2 transection, 253. Mean vessel element length, 218 μm. Mean vessel wall thickness, 3.0 μm. Perforation plates simple. Lateral wall pitting of vessels consisting of alternate circular pits 3 μm diam. Imperforate tracheary elements are all tracheids (Fig.

38), with pits 3 μm diam. Tracheid diameter at widest point, 18 μm. Mean tracheid length, 312 μm. Mean tracheid wall thickness, 3.0 μm. Axial parenchyma scanty vasicentric, less commonly diffuse (Fig. 36). Axial parenchyma in strands of two cells. Multiseriate and uniseriate rays equally common (Fig. 37). Mean multiseriate ray height, 398 μm. Mean multiseriate ray width at widest point, 2.8 cells. Mean uniseriate ray height, 114 μm. A few series of procumbent cells present in the central portions of the multiseriate rays; the remainder of ray cells upright or square. Ray cell wall thickness, 2.0 μm. All pits among ray cells bordered as seen in sectional view. No crystals observed. Wood nonstoried (Fig. 37).

SELAGINACEAE

Selago thunbergii Choisy, *Carlquist 8061* (RSA), cultivated in Kirstenbosch Botanical Garden, Cape Province, South Africa (Figs. 41, 42). Growth rings absent or only indistinctly demarcated. Vessels mostly solitary; mean number of vessels per group, 1.43. Vessels rounded as seen in transection. Mean vessel lumen diameter at widest point, 20 μm. Mean number of vessels per mm² transection, 348. Mean vessel element length, 221 μm. Mean vessel wall thickness, 2.0 μm. Perforation plates simple. Lateral wall pitting alternate, pits about 3 μm diam. Helical thickenings present on vessels (Fig. 42) and vasicentric tracheids (Fig. 41). Imperforate tracheary elements are libriform fibers with simple slitlike pits; some vasicentric tracheids are also present. Mean libriform fiber diameter at widest point, 17 μm. Mean libriform fiber length, 274 μm. Mean libriform fiber wall thickness, 2.5 μm. Axial parenchyma absent. Rays absent (or represented in later formed wood by upright cells virtually indistinguishable from libriform fibers). Crystals absent. Wood nonstoried.

Walafrida nitida E. Mey., *Carlquist 8062* (RSA), cultivated in Kirstenbosch Botanic Garden, Cape Province, South Africa (Figs. 39, 40, 43). Growth rings absent or indistinct (Fig. 39). Vessels solitary or in small groupings (Fig. 39); mean number of vessels per group, 2.7. Mean vessel lumen diameter at widest point, 22 μm. Mean number of vessels per mm² transection, 398. Mean vessel element length, 223 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. Lateral wall pits of vessels bearing alternate circular pits about 3 μm diam. vertically, 4 μm horizontally. Helical thickenings present on vessels (Fig. 43) and vasicentric tracheids. Imperforate tracheary ele-

ments mostly fiber-tracheids with vestigially bordered pits; a few vasicentric tracheids present. Fiber-tracheids apparently nucleated. Axial parenchyma absent. Rays absent (Fig. 40). Crystals not observed. Wood nonstoried.

DISCUSSIONS OF SYSTEMATIC RELATIONSHIPS

ERICALES

Although data on iridoids are not available for all families of Ericales (Table 1), the presence of iridoids is widespread in this order. Ericales in the sense of Dahlgren (1975) have tenuinucellate ovules with one integument and nuclear endosperm. All of the Ericales have primitive wood features: vessels with scalariform perforation plates; tracheids (rather than fiber-tracheids or libriform fibers); diffuse axial parenchyma; and Heterogeneous Type I or Type IIA rays. Presence of libriform fibers (or fiber-tracheids) together with vasicentric tracheids in the subfamily Arbutoideae of Ericaceae represents a simple step away from the primitive wood configuration as a result of tracheid dimorphism (Carlquist, 1988c). The families of Ericales listed in Table 1 share these primitive wood features with choripetalous ericalean families: Actinidiaceae, Clethraceae, and Empetraceae. The choripetalous family Aquifoliaceae has primitive wood features like those of the Ericales listed, and in addition has the three embryological character states listed for Ericales. Thorne (1976) placed Aquifoliaceae in Ericales.

CORNALES

An interesting feature of Dahlgren's (1975) system is the grouping in Cornales of families that in other systems have been scattered in various portions of "Rosales," "Saxifragales," or other orders. The orders to which the families of Dahlgren's Cornales were previously referred are not close to each other in most systems. Dahlgren's Cornales include iridoid-bearing bicarpellate families; the embryological features agree with those of Ericales except that, in contrast, cornalean families have cellular rather than free nuclear endosperm development. The choripetalous families of Dahlgren's Cornales include Alangiaceae, Cornaceae, Davidiaceae, Escalloniaceae, Garryaceae, Icacinaceae, and Nyssaceae. Notably absent, compared with earlier concepts of Cornales, are Araliaceae and Apiaceae, which lack iridoids. The sympetalous families of Cornales do not form a coherent assemblage—they appear to be isolated instances of sym-

petaly within a predominantly choripetalous order. Columelliaceae have been most commonly placed in Scrophulariales in the past (see Stern et al., 1969). Columelliaceae have primitive woods like those of Escalloniaceae and Hydrangeaceae, as stressed by Stern et al. (1969). Wood definitely is a key to relationships in this case.

Alseuosmiaceae also have very primitive wood (Dickison, 1986). All but one species are rayless (Dickison, 1986). The raylessness is not indicative of relationship, but rather may indicate derivation from an herbaceous ancestry, as in other rayless groups. Rays do occur in one species of Alseuosmiaceae: *Crispiloba disperma* (S. Moore) van Steenis. Ancestry of the family as a whole may not be herbaceous. Wood anatomy suggests that Alseuosmiaceae are related to Hydrangeaceae (Dickison, 1986), but Columelliaceae may not be the family closest to Alseuosmiaceae.

Stylidiaceae are a curious family once placed in close proximity to other inulin-containing families: Asteraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae. Dahlgren's (1975) decision to place more confidence in iridoids (absent in those families but present in Stylidiaceae) than inulins as a phylogenetic indicator resulted in transfer of Stylidiaceae to an entirely new systematic position. The wood of Stylidiaceae (very few species of which are woody) has several peculiarities. The cambium originates outside the scattered bundles of the stem (which resembles that of a monocotyledon). The cambium acts unilaterally: it produces secondary xylem to the inside but no secondary phloem to the outside. Wood of Stylidiaceae contains tiny strands of interxylary phloem and is rayless. The presence of fiber-tracheids rather than libriform fibers in wood of Stylidiaceae represents retention of a single primitive character state in a wood otherwise highly specialized. Because of this, attempting to use wood anatomy as a basis for relating Stylidiaceae to the other families of Cornales, which have very primitive wood, is difficult. Data from wood anatomy do not negate a relationship between Stylidiaceae and the other families placed in Cornales, however.

LOASALES

The herbaceous habits, peculiar trichomes, and inferior ovary of Loasaceae are distinctive features that have made them difficult to place with woody hypogynous dicotyledonous families. Loasaceae are minimally sympetalous. The various phylogenetic treatments often select a choripetalous order as closest to the family, but most systems also emphasize the distinctiveness of the monofamilial order. Scalariform perforation plates are occasional in secondary xylem, and this probably is indicative of paedomorphosis. The scalariform condition is present in the primary xylem, but is perpetuated irregularly into secondary xylem through paedomorphosis. Primitiveness of loasaceous wood is indicated by possession of tracheids and diffuse axial parenchyma. These various remnants of a primitive wood configuration suggest that Loasales are not far from such orders as Cornales or Dipsacales. The many indicators of paedomorphosis, especially those of rays, suggest that whatever its closest ally, the immediate ancestor of Loasaceae was likely herbaceous.

DIPSACALES

The order Dipsacales as constituted by Dahlgren (1975) contains unusually disparate contents with respect to wood anatomy. The wood anatomy of Caprifoliaceae (including *Viburnum* but excluding *Sambucus*) is quite primitive. In fact, the wood of Caprifoliaceae is essentially like that of such Hydrangeaceae as *Philadelphus*. Vining and lianoid Caprifoliaceae have some acceleration in wood anatomy (simplification of perforation plates), but these changes are minor alternations of the basic plan.

Sambucus, the sole woody genus of Adoxaceae, has very specialized wood that features vessels with simple perforation plates, vascular tracheids (tracheids at the end of a growth ring), libriform fibers, vasicentric axial parenchyma, Heterogeneous Type IIB rays, and storied wood structure. On the basis of wood anatomy, placement of *Sambucus* in Caprifoliaceae, Escalloniaceae, Hydrangeaceae, or any of the Cornales of Dahlgren (1975) would not be indicated. While wood anatomy by itself cannot conclusively indicate relationship, the gap between *Sambucus* and the families named, all of which have notably primitive wood, must be emphasized. The evidence speaks clearly for recognition of *Sambucus* in a family separate from Caprifoliaceae.

Dipsacaceae have woody representatives in dry situations (e.g., Canary Islands, Aegean Islands). As one might expect in such sites, simple perforation plates have evolved in these representatives. Imperforate tracheary elements of Dipsacaceae, however, are tracheids. Axial parenchyma is diffuse. These two features are characteristic of primitive woods and would not be unexpected if Dipsacaceae were a phylad related to Caprifoliaceae that has evolved in drier conditions.

Valerianaceae and Calyceraceae have simple perforation plates, libriform fibers rather than tracheids, and scanty vasicentric axial parenchyma. These families, therefore, represent a higher level of specialization than Dipsacaceae. That does not rule out relationship, but it emphasizes that these families are distinct from those with more primitive woods in Dipsacales (or other orders).

GOODENIALES

In the Dahlgren (1975) system, Goodeniaceae are no longer placed with Campanulaceae and Lobeliaceae, although compelling evidence for placing these three families together on a line leading to Asteraceae has been presented by Olmstead & Palmer (1992). Goodeniaceae have wood features very similar to those of Dipsacaceae in level of specialization: simple perforation plates, tracheids, and diffuse parenchyma. This does not necessarily imply a phylogenetic relationship between Dipsacaceae and Goodeniaceae. It does suggest a similar phylesis: evolution of a group with basically primitive wood in areas with climates strongly seasonal with respect to rainfall. Because Goodeniaceae have relatively primitive wood, they cannot be derived from any phylads that have highly specialized wood (e.g., Valerianaceae). This must be considered in cladistic hypotheses that involve Goodeniaceae.

GENTIANALES

The order Gentianales as defined by Dahlgren (1975) appears to be relatively homogeneous according to the data in Table 1. Wood features common to the families include simple perforation plates and fiber-tracheids (in some species, tracheidlike). Although vasicentric parenchyma occurs in some Gentianales, banded apotracheal axial parenchyma (rarely found in the families that lack iridoids) is common in the order. Vesturing and storying are uncommon in Gentianales, but may be found in most of the families. Because few Gentianaceae are woody, the lack of data on vesturing in that family may be a sampling artifact. Rays are Heterogeneous Type IIA or IIB (or, in certain Gentianaceae, a paedomorphic derivative of one of these types). Unitegmic tenuinucellate ovules are universal in the order. Nuclear endosperm (otherwise nearly restricted to Plumbaginales and Primulales in the sympetalous families) characterizes Gentianales. Perhaps most noteworthy to the concept of Gentianales is the presence of intraxylary phloem—strands of phloem between the primary xylem and the pith in stems. This feature occurs in all of the gentianalean families except Rubiaceae.

Do Rubiaceae fit well into the concept Gentianales? Rubiaceae lack intraxylary phloem, but they do have elongate glandular trichomes ("colleters") on stipules. These stipular glandular trichomes characterize the other gentianalean families (Metcalfe & Chalk, 1950).

Complicating the use of wood features in placing the Rubiaceae is the diversity of wood in the family. This diversity can be shown within a single genus. In *Coprosma montana* Hillebr. (Fig. 1), axial parenchyma is apotracheal banded, diffuse, and scanty vasicentric, all coexisting within the same wood. In another Hawaiian species, *C. foliosa* A. Gray (Fig. 3), axial parenchyma is predominantly scanty vasicentric, with a little diffuse parenchyma. In *C. montana* rays are Paedomorphic Type I, but elsewhere in the genus, less abundant upright ray cells, ranging to predominance of procumbent cells (= Heterogeneous type IIB, verging on Homogeneous Type I), may be found in the eight *Coprosma* species treated with respect to wood anatomy by Meylan & Butterfield (1978). Heterogeneous Type II rays also occur in Rubiaceae (Metcalfe & Chalk, 1950).

Imperforate tracheary elements in *Coprosma* are fiber-tracheids in which pit borders are small but definitely present (Fig. 4). However, in *Galium* (Figs. 5–7), imperforate tracheary elements are tracheids, with relatively large, fully bordered pits (Figs. 6, 7). However, in most Rubiaceae, pits on imperforate tracheary elements range from moderately to vestigially bordered to simple (Koek-Noorman, 1969a, b, 1970, 1972; Koek-Noorman & Puff, 1983), so that a complete range in imperforate tracheary elements is present. In *Galium*, woods are storied (new report for the genus and for the family: Fig. 6). *Galium* is probably a representative of an herbaceous phylad (the tribe Rubieae) that has radiated into more moderate climates where secondary woodiness has occurred. This is probably true for *Rubia fruticosa* L. also (data from Koek-Noorman, 1970). Both *Galium catalinense* A. Gray and *Rubia fruticosa* have upright ray cells only (Fig. 8, right), and both species are thus nearly rayless. *Galium* and *Rubia* show several features that differ from those in other Rubiaceae, demonstrating the diversity of the family.

Raphides are present in ray cells of *Galium* (Fig. 8: new report for the genus) and other Rubiaceae (Koek-Noorman, 1969a), yet rhomboidal crystals occur in ray cells in other species of the family

(Koek-Noorman, 1969a). Raphides in ray cells have not been reported for other families of sympetalous dicotyledons. Presence of tracheids and of rare, scattered (and sometimes malformed) scalariform perforation plates in Rubiaceae are indicators of primitive character states in the wood.

The wood diversity of Rubiaceae presents difficulties when discussing the concept Gentianales, because the other families have wood that is much more uniform. A wider range of character states need not exclude Rubiaceae from Gentianales. The wider range in Rubiaceae may (in part) be related to the large size of the family, although the examples given within the genus *Coprosma* tend to counter the idea that diversity in wood features is proportional to the size of the family. Gentianales might be slightly more coherent if Rubiaceae were excluded, but in that case, Rubiaceae would have to be located in a neighboring monofamilial order, a treatment very close to including the family within Gentianales.

OLEALES

Wood of Oleaceae has been studied thoroughly by Baas et al. (1988), who demonstrated the great diversity of many wood features in the family. As with Rubiaceae, this diversity tends to mask the systematic affinities of the family. For example, imperforate tracheary elements of Oleaceae range from tracheids to fiber-tracheids with vestigial borders on pits to libriform fibers with pits apparently simple. Baas et al. (1988) concluded that Oleaceae belong in or near Gentianales, a conclusion much like that of Mennega (1980); however, citation of wood features to support this placement reveals nothing decisive. The chemical data of Hegnauer (1971) seem more persuasive than wood data. Separation of Oleaceae in their own order seems advisable under the circumstances. The analysis of Coulaud (1988) supports this position.

SCROPHULARIALES

Buddlejaceae traditionally were regarded as a tribe within Loganiaceae. As a family, Buddlejaceae were placed by Dahlgren (1975) among Gentianales because of iridoid content. However, as the data of Table 1 indicate, Buddlejaceae differ from Gentianales in a number of significant respects. The wood anatomy of Buddlejaceae (as tribe Buddlejeae of Loganiaceae) was summarized by Mennega (1980). Illustrations are offered here because wood anatomy of Buddlejaceae has not been figured extensively heretofore, and the features shown indicate the probable affinities of the family. The

imperforate tracheary elements of Buddlejaceae are libriform fibers. Because the imperforate tracheary elements are not tracheids, grouping of vessels in response to xeromorphy is marked in *Buddleja*, species of which range from mesic to very dry sites. In *B. globosa* Hope (Fig. 9), vessels are relatively little grouped. The bands of latewood vessels of *B. parviflora* HBK (Fig. 13) form extensive aggregations as tangential bands, as do (much less conspicuously) the latewood vessels of *B. utahensis* Cov. (Fig. 17). Some latewood vessels are as narrow as libriform fibers (Fig. 20, left). Vasicentric tracheids are present in all three species illustrated. Vasicentric tracheids in *Buddleja* are somewhat more common in latewood than in early wood. Helical thickenings are common in vessels of *Buddleja*, although lacking in some species (*B. americana* L., *Hutchinson 3406*, U. C. Berkeley Botanic Garden). In *B. globosa* (Fig. 11) and *B. parviflora* (Fig. 15), all vessels possess helical thickenings. In *B. utahensis*, wide vessels lack helical thickenings (Fig. 19), whereas narrow vessels possess them (Fig. 21). Axial parenchyma in *Buddleja* is scanty vasicentric. No banded parenchyma and no diffuse parenchyma occur. Rays of *Buddleja* are uniformly Heterogeneous Type IIA or IIB (Figs. 10, 14, 18). Procumbent cells predominate in the rays, as shown in tangential section in Figures 10, 14, and 18, and in radial section in Figures 12, 16, and 21 (note horizontal axis of rays oriented vertically in Figs. 12 and 21). Crystals in rays of *Buddleja* are common in most species. In *B. globosa*, crystals are rhomboidal to somewhat elongate (Fig. 12). In *B. parviflora*, crystals are not elongate, and some are paired in mirror-image fashion (Fig. 16). In *B. utahensis*, the crystals are clearly elongate (Fig. 21).

In embryological features, Buddlejaceae differ from Gentianales by having cellular endosperm, a feature characteristic of Scrophulariales and Lamiales. The lack of borders on pits of imperforate tracheary elements allies Buddlejaceae with Scrophulariales or Lamiales: libriform fibers occur in Gentianales only in certain Rubiaceae, and Rubiaceae are, as mentioned above, probably best placed in Gentianales. Axial parenchyma in Buddlejaceae is typical of that found in Scrophulariales or Lamiales (scanty vasicentric), and banded parenchyma, frequent in Gentianales, is absent.

Other features of Buddlejaceae are not decisive: elongate to rhomboidal crystals in rays are frequently found in families of Gentianales, Lamiales, and Scrophulariales. Lack of vesturing in vessel pits of Buddlejaceae is not decisive because in no sympetalous family of dicotyledons does vesturing

characterize large portions of a family. In sum, Buddlejaceae clearly should be transferred from Gentianales to Scrophulariales or Lamiales. The fruit type of Buddlejaceae may provide the decisive feature: it is capsular, with many ovules, as in Scrophulariales, rather than composed of nutlets, each with a single ovule, as in Lamiales. Therefore, Buddlejaceae most likely belong in Scrophulariales, and I have included them in that order in Table 1 rather than following Dahlgren's treatment.

Evidence from wood anatomy indicates that Scrophulariaceae sensu lato are more diverse than many current systematic treatments indicate. The diversity need not result in segregation of subfamilies as independent families, although the evidence from wood anatomy does seem to indicate that for two families, Globulariaceae and Selaginaceae.

Raylessness occurs in two subfamilies of Scrophulariaceae, Rhinanthoideae and Antirrhinoideae, of Wettstein's (1891) system. All *Calceolaria* species I have investigated prove to be rayless, as shown for *C. adscendens* Lindl. in Figures 22 and 23; Metcalfe & Chalk (1950) also reported the genus as rayless (no species given). Other distinctive features of the wood of *Calceolaria* include vessels in radial multiples (Fig. 22) and absence of axial parenchyma. The wood is storied, although not conspicuously so (Fig. 23). Axial parenchyma absence is common in rayless woods (Carlquist, 1970a), a condition perhaps related to the relatively thin woody cylinders accumulated by most rayless species. More significantly, raylessness is an excellent indicator of herbaceous ancestry (Carlquist, 1970a), although exceptions may occur. *Calceolaria* is a predominantly herbaceous genus (Wettstein, 1891), so that secondary woodiness is probable on numerical grounds alone; shrubs in the genus are short-lived and herblike.

Raylessness in *Hebe* (Figs. 24–26) has been known for several decades (Metcalfe & Chalk, 1950; Meylan & Butterfield, 1978). In *Hebe*, vessels are in radial multiples, although the groupings are small, and solitary vessels are common (Fig. 24). Axial parenchyma is absent. Wood is nonstoried (Fig. 25). Imperforate tracheary elements have vestigial borders on pits (Fig. 26), as reported for *H. salicifolia* (Forst. f.) Pennell by Meylan & Butterfield (1978). Some pits in imperforate elements in *H. elliptica* Pennell are apparently simple, although others are vestigially bordered (Fig. 26), a fact revealed by the air content of the cell shown in Figure 26. Worthy of investigation in *Hebe* is whether pits are simple as opposed to bordered, both on fibriform cells in "potential ray areas" and on imperforate tracheary elements in

fascicular areas. *Hebe* seems to be a woody derivative of *Veronica*, or a *Veronica*-like ancestor. *Hebe* and *Veronica* form a distinctive group within tribe Digitaleae of subfamily Rhinanthoideae (Wettstein, 1891). Raylessness is not evidence for close relationship between *Hebe* and *Calceolaria*, and indeed, the two genera are widely separated in Wettstein's (1891) system for the family. Further comments on the significance of raylessness are offered in a concluding section of this paper devoted to correlations between habit and wood anatomy.

Paulownia has been a genus of uncertain position, referred either to Bignoniaceae or Scrophulariaceae or even an intermediate position (for a history, see Armstrong, 1985). This situation has not received comment with respect to wood anatomy. *Paulownia* wood is illustrated here (Figs. 27–29), along with a genus of Bignoniaceae with some similarities, *Catalpa* (Figs. 31, 32), and, for comparison, a genus (*Tecoma*) with wood typical of Bignoniaceae (Figs. 33, 34). *Paulownia* has been compared to *Catalpa* by some authors.

Paulownia is notable for its well-marked growth rings (Fig. 27). The large earlywood vessels are embedded in a large quantity of initial axial parenchyma. When viewed in longitudinal section, this initial parenchyma is composed of very thin-walled cells in strands of one to two cells (Fig. 28, left; Fig. 29, left). Latewood vessels of *Paulownia* are associated with aliform or aliform-confluent axial parenchyma (likewise in strands of one to two cells when seen in longitudinal section). Rays are narrow, multiseriate, and composed of procumbent cells (Figs. 28, 29) and are Homogeneous Type II in the Kribs (1935) system. This description accords with the Metcalfe & Chalk (1950) reports. None of the axial parenchyma or ray features cited have been reported in Scrophulariaceae (Metcalfe & Chalk, 1950; Michener, 1981, 1986). In Scrophulariaceae, axial parenchyma is scanty vasicentric, and rays are Heterogeneous Type I or Type II. Conceding that the degree of parenchymatization of *Paulownia* wood is unique in arboreal sympetalous dicotyledons, the pattern of parenchymatization is not like that of other genera. For example, in *Faradaya* of the Verbenaceae (Fig. 30), a wood with abundant axial parenchyma, parenchyma takes the form of wider rays and of axial parenchyma that is not adjacent to vessels. Vessels are sheathed with libriform fibers rather than axial parenchyma. To be sure, these features of *Faradaya* may be related to its lianoid habit.

Catalpa (Figs. 31, 32) of the Bignoniaceae has well-demarcated growth rings and, like *Paulownia*,

large quantities of initial axial parenchyma. The latewood vessels of *Catalpa* (Fig. 31) form large aggregations that are associated with scanty vasicentric axial parenchyma. Rays of *Catalpa* (Fig. 32) are Heterogeneous Type IIB, transitional to Homogeneous Type II. Thus, *Catalpa* has wood more like that of Scrophulariaceae than does *Paulownia*. *Paulownia* wood is more similar to that of Bignoniaceae than to that of *Catalpa*. This is underlined by the aliform-confluent axial parenchyma (Fig. 33) of *Tecoma*, which forms strands of four to five cells in longitudinal section (Fig. 34). Rays of Bignoniaceae are not always storied in Bignoniaceae, as shown for *Tecoma* (Fig. 34), but they are storied in many genera. The wood data on Bignoniaceae and Scrophulariaceae of Outer & Veenendal (1981) support the above conclusions.

The South African genus *Oftia* has mostly been placed in Myoporaceae (for a summary, see Dahlgren & Rao, 1971). *Oftia* has the following wood features: perforation plates simple (but often double); libriform fibers septate; axial parenchyma scarce; and upright cells predominant in rays (Carlquist & Hoekman, 1986b). The upright ray cells in *Oftia* are likely indicative of paedomorphosis, whereas the predominance of procumbent cells in rays of Myoporaceae is indicative of a woody ancestry for the family. The septate libriform fibers and the scarce, scanty vasicentric parenchyma of *Oftia* suggest relationship other than to Myoporaceae, in which fiber-tracheids and more abundant vasicentric axial parenchyma are present (Carlquist & Hoekman, 1986b). This supports the opinion of Dahlgren & Rao (1971) that *Oftia* belongs in Scrophulariaceae.

Leucophyllum has often been considered to belong to the Scrophulariaceae. Niezgoda & Tomb (1975) claim a link between *Leucophyllum* and Myoporaceae on the basis of pollen. *Leucophyllum* has vessels with prominent helical thickenings; vascular tracheids abundant in latewood, producing a transition to vasicentric tracheids, as in some Lamiaceae (Carlquist, 1992); scanty vasicentric axial parenchyma; and abundant fibriform vessel elements. These features differ from those of Myoporaceae (see above under *Oftia*). Reexamination of the familial location of *Leucophyllum* is therefore urged.

Globulariaceae are a small group of genera sometimes placed within Scrophulariaceae, and sometimes recognized as a segregate family situated close to Scrophulariaceae. Because material was available (see New Data, above), I have included original data on wood of Globulariaceae here. One significant feature of *Globularia* wood with respect to systematics is the presence of tracheids (Fig. 38) rather than fiber-tracheids or libriform fibers. Presence of tracheids in wood of *Globularia* is related to lack of vessel grouping (Fig. 35), for reasons proposed earlier (Carlquist, 1984a). Another significant feature of *Globularia* wood is the presence of diffuse axial parenchyma (Fig. 36) in addition to scanty vasicentric parenchyma. Rays are Heterogeneous Type IIA (Fig. 37). Tracheids and diffuse axial parenchyma represent maximally primitive character states and are expressions more primitive than found in other families of Scrophulariales. One can conclude that Globulariaceae are a distinct family. The primitiveness of wood in this family means that it cannot be derived from scrophularialean families with more specialized wood, and this should be taken into account in phyletic work. Further studies to assess the precise relationships of this neglected family are needed.

Another small group of genera sometimes included within Scrophulariaceae is represented by the segregate family Selaginaceae. As with Globulariaceae, availability of wood has led to presentation of original information (see New Data, above). The specimens studied differ, although not greatly, with respect to imperforate tracheary elements: *Walafrida nitida* has fiber-tracheids with vestigial pit borders, whereas *Selago thunbergii* has libriform fibers—the pits are apparently simple. Axial parenchyma is absent, a condition that may be related to raylessness, as with *Calceolaria* and *Hebe* mentioned above. The imperforate tracheary elements may be nucleated (the deposits observed suggest either nuclei or residues formed as a result of prolonged duration of protoplasts). There are pronounced helical thickenings in the vessels of *Selago thunbergii* (Figs. 41, 42) and *Walafrida nitida* (Fig. 43); these are similar to those seen in a scattering of Scrophulariaceae from dry localities. Although vascular tracheids (formed at the ends of growth rings) can be seen in some Scrophulariaceae, Selaginaceae are the only family in which typical vasicentric tracheids have thus far been observed. That feature, in addition to the raylessness, reinforces recognition of this group at a familial level. As with Globulariaceae, affinities of Selaginaceae need to be investigated using modern DNA techniques.

Outer & Veenendal (1983) reported on one species of Pedaliaceae. They presented a table with qualitative features for eight species of Acanthaceae, 22 species of Bignoniaceae, but only one atypical species of Scrophulariaceae—*Paulownia tomentosa* (Thunb.) Sond. They concluded that Pedaliaceae are close to Bignoniaceae. When a

wider range of Pedaliaceae is looked at (Carlquist, 1987b) and compared with all other families of Scrophulariales, the situation changes. The apotracheal parenchyma bands of *Sesamothamnus* are the result of fiber dimorphism and are not related to the aliform-confluent bands in wood of Bignoniaceae. All of the wood features of Pedaliaceae may be found in Scrophulariales (and, for that matter, in Scrophulariaceae), but Pedaliaceae are not really closer to one family of Scrophulariales than another on the basis of wood anatomy. The similarity in pollen between Martyniaceae and Pedaliaceae is intriguing. However, more studies are needed to resolve interrelationships of the scrophularialean families.

LAMIALES

The Lamiales could once be described as the families Lamiaceae and Verbenaceae. However, segregate families have been recognized, and wood anatomy tends to support these. Studies on phylogeny of Lamiaceae by Cantino (1992) suggest that Lamiaceae may be a collection of independent derivatives from Verbenaceae. If this is true, Lamiaceae must be united with Verbenaceae, or else Lamiaceae may be subdivided into several families representing these independent phylads. Unfortunately, Lu (1990) did not analyze the segregate families of Verbenaceae, so his cladistic analysis of Lamiales is not discussed here.

Avicenniaceae are one of the families frequently segregated from Verbenaceae. Avicenniaceae have successive cambia (Fig. 44) with distinctive bands of sclerenchyma in the conjunctive tissue (Figs. 44, 45). Vessels are in radial multiples (Fig. 44). Imperforate tracheary elements are nonseptate libriform fibers. Crystals are abundant in rays (Fig. 45). In Verbenaceae, cambia are normal; vessels are in clusters; imperforate tracheary elements are mostly septate libriform fibers; crystals are reported in ray cells only in *Vitex* (Carlquist, 1988a), but even in that genus they are rare or absent (Meylan & Butterfield, 1978). These distinctions, added to those from gross morphology, support segregation of Avicenniaceae from Verbenaceae.

Chloanthaceae (= Dicrastylidaceae of some authors) are similar to Avicenniaceae in having successive cambia. The occurrence of successive cambia in Chloanthaceae is not evidence of relationship to Avicenniaceae. In Chloanthaceae, phloem is frequently in continuous tangential bands rather than in isolated strands, and no sclerenchyma bands occur in the conjunctive tissue (Carlquist, 1981a). Imperforate tracheary elements in Chloanthaceae

are fiber-tracheids rather than libriform fibers. Verbenaceae have libriform fibers; Metcalfe & Chalk (1950) reported fiber-tracheids in *Petraea arborea* HBK (Verbenaceae), but my material of *Petraea* has only libriform fibers. Upright ray cells predominate in rays of Chloanthaceae (Carlquist, 1981a) but are only on ray margins in Verbenaceae. The differences between wood of Chloanthaceae and Verbenaceae sensu stricto are sufficient to support segregation of Chloanthaceae.

Stilbaceae have frequently been considered a subfamily of Verbenaceae, but several recent authors have recognized them as a segregate family (for a history, see Carlquist, 1986). Wood of Stilbaceae has simple plus scalariform perforation plates; vessels in long radial multiples; an abundance of fibriform vessel elements; either fiber-tracheids or libriform fibers, notably thick-walled; scarce vasicentric axial parenchyma; and Heterogeneous Type IIA rays. Verbenaceae have only simple perforation plates (aberrant scalariform perforation plates exceptionally: Meylan & Butterfield, 1978); vessel elements rarely fibriform; vessels solitary or in clusters; libriform fibers (often septate and thinner-walled than in Stilbaceae); scanty vasicentric axial parenchyma; and rays Heterogeneous Type IIA or IIB transitional to Homogeneous Type II.

The features just cited for Stilbaceae are also characteristic of Retziaceae (Carlquist, 1986). This confirms the opinion of Dahlgren et al. (1979) that the two families are closely related. My conclusion (Carlquist, 1986) is that the two families should be united.

PLUMBAGINALES

Wood of Plumbaginaceae (Table 1) has been little studied to date because few species of the family are woody. Features presently known show that the wood features are similar to those of other sympetalous dicotyledon families. The wood of this family, then, is not helpful in demonstrating affinities of Plumbaginaceae.

EBENALES

Ebenaceae are the only family of Ebenales to be considered here because other families in the order are choripetalous or nearly so. There obviously is a bias introduced by this selection. However, the question at hand is whether Ebenaceae are at all related to other choripetalous families of dicotyledons. Ebenaceae have a distinctive combination of wood features (Figs. 46, 47). Axial parenchyma is diffuse to banded (Fig. 46), and

both of these types are infrequent in the other sympetalous families. The imperforate tracheary element type for the family is the fiber-tracheid. Rays are diverse: Heterogeneous Type II, Heterogeneous Type III, and Homogeneous Type I (Fig. 47); only the first of these is common in other sympetalous families. Storied wood structure, common in Ebenaceae (Fig. 47), occurs commonly in only a few of the other sympetalous families. Ebenaceae differ from most other sympetalous families in having bitegmic ovules (Table 1). This underlines the fact that neither wood nor other features indicate close relationship between Ebenaceae and the other sympetalous families.

PRIMULALES

Primulales are united on the basis of embryology (Table 1): the three families have bitegmic tenuinucellate ovules and nuclear endosperm. All three families have libriform fibers. Primulaceae are reported here on the basis of Hawaiian species of *Lysimachia* only. The rayless wood and diffuse axial parenchyma of *Lysimachia* are not representative for the order as a whole. Myrsinaceae and Theophrastaceae are close to each other on the basis of wood anatomy. The concept of Primulales as constituted by Dahlgren (1975) is not countered by wood data if one concedes that *Lysimachia* is not representative. The distinctive wide rays of Myrsinaceae and Theophrastaceae, in which procumbent cells predominate, can be called transitional between Heterogeneous Type IIB and Homogeneous Type II. Rays of this sort are not characteristic of other sympetalous families.

ASTERALES

The affinities of Asteraceae have traditionally been claimed (e.g., in the Engler system) to be with families that contain inulin: Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae. Inulin characterizes only some Asteraceae. Dahlgren's (1975) decision to disassemble the alliance cited above was based on a different chemical character, iridoid presence or absence. The families placed near Asteraceae in the Engler system all lack iridoids except for Goodeniaceae and Stylidiaceae (Table 1).

Embryologically, Asteraceae agree with virtually all sympetalous families except Plumbaginales, Ebenales, and Primulales. Asteraceae are remarkably uniform (considering the size of the family) with respect to characters of major evolutionary significance. The diversity within woods of Asteraceae is mostly related to ecology; this ecological range is so distinctive that it inspired my earliest

ideas about how wood anatomy is related to ecology (Carlquist, 1966b). Although Baas (1986) has reported vestigial borders on pits of imperforate tracheary elements of one species of Asteraceae, the family as a whole is still characterized by having libriform fibers (which have simple pits, according to the definitions of the IAWA Committee on Nomenclature, 1964). With respect to similarities in wood anatomy between Asteraceae and other families, the features characteristic of wood of Asteraceae (Table 1) are all found in woods of Apiaceae, Calyceraceae, Campanulaceae, Lamiaceae, and Scrophulariaceae. A wood sample of one of these families would not yield any diagnostic features different from those of wood of Asteraceae. This is noteworthy in view of the results of Olmstead & Palmer (1992), who find that Goodeniaceae, Campanulaceae, Lobeliaceae, and Calyceraceae are on the clade leading to Asteraceae. Goodeniaceae have wood somewhat more primitive than that of the other families in this clade. If that difference could be explained, there would be no evidence from wood anatomy conflicting with the views of Olmstead and Palmer on the phylogeny of Asteraceae.

CAMPANULALES

The three families of Campanulales (Campanulaceae, Lobeliaceae, and Pentaphragmataceae) recognized by Dahlgren (1975) form a coherent group on embryological grounds (Table 1). The wood anatomy of Campanulales represents variations on the same basic plan, because these variations are due to paedomorphosis. Campanulaceae have scalariform perforation plates in primary xylem (Bierhorst & Zamora, 1965); through paedomorphosis, this perforation plate type has been extended into the secondary xylem. Shulkina & Zikov's (1980) figures for woods of Campanulaceae are clearly indicative of this. Ancestrally in Campanulales there doubtless are scalariform perforation plates in primary xylem. This is more primitive than a condition in which there are simple perforation plates in both primary and secondary xylem, exemplifying the "refugium" theory of Bailey (1944). By means of paedomorphosis, primitive primary xylem characteristics may be extended into secondary xylem. Campanulaceae show more paedomorphosis with respect to perforation plates than do Lobeliaceae, in which scalariform perforation plates are virtually absent from secondary xylem (Carlquist, 1962a, 1969a). Pentaphragmataceae, on the other hand, show the greatest degree of paedomorphosis: scalariform perforation plates are characteristically present throughout the secondary xylem. The secondary xylem is also ray-

less (a paedomorphic feature), and septate fiber-tracheids are present. One can hardly doubt that *Pentaphragma* is an herb with a moderate amount of secondary xylem, so paedomorphosis, related to wood development in herbs, is definitely represented in this genus. The rays of Campanulaceae and Lobeliaceae are paedomorphic (Carlquist, 1962a, 1969a).

As mentioned above, Campanulales have no wood features that are not found in Asteraceae. Interesting in this regard are the occasional aberrant scalariform perforation plates reported in wood of Asteraceae (Carlquist, 1960a, 1965a, b; Meylan & Butterfield, 1978). These occasional scalariform perforation plates are indicative of paedomorphosis and show that primary xylem of Asteraceae retains, in at least some phylads, scalariform perforation plates. Many Asteraceae have Paedomorphic Type I rays (Carlquist, 1966b). These examples show that the evolutionary level of wood of Asteraceae and the intervention of paedomorphosis shown by the wood of Asteraceae are like what we have seen in Campanulaceae and Lobeliaceae.

SOLANALES

I have recognized segregate families of Solanaceae here using the scheme of Hunziker (1979). Hunziker recognized a constellation of families close to Solanaceae: Duckeodendraceae, Goetzeaceae, Nolanaceae, and Sclerophylacaceae (the last of these is entirely herbaceous, and therefore not considered here). These families differ mainly on the basis of embryo, seed, and fruit types. Wood data support recognition of at least one of these: *Duckeodendron* has abundant vasicentric axial parenchyma, banded apotracheal axial parenchyma, and Heterogeneous Type I rays, none of which typify Solanaceae sensu stricto. Wood anatomy of Goetzeaceae and Nolanaceae falls within the range found in Solanaceae. However, this can be considered evidence that these two families are very close to Solanaceae, if one chooses to recognize them as separate from Solanaceae.

The family closest to Solanaceae and their segregate families is Convolvulaceae. Notable in this regard is the occurrence of intraxylary phloem in primary stems of all species of these families. The occurrence of cellular endosperm in Convolvulaceae is one of the few reasons for excluding this family from Solanales.

BORAGINALES

The Boraginales and Solanales of the Dahlgren (1975) system are problematic because, as shown in Table 1, Dahlgren included Polemoniaceae in Solanales, yet families often considered close to Solanales, such as Boraginaceae and Hydrophyllaceae, fall into his Boraginales. Although other types of evidence may show sharper demarcation among orders containing these families and indicate optimal reassignments, evidence from wood cannot be used to segregate Hydrophyllaceae and Boraginaceae from an order that contains Polemoniaceae. Boraginaceae, Hydrophyllaceae, and Polemoniaceae are families in which certain wood features show considerable diversity. For example, in Boraginaceae, axial parenchyma may be diffuse, diffuse-in-aggregates, aliform, confluent, and even vasicentric (either abundant or, in *Echium*, scanty). In Hydrophyllaceae, imperforate tracheary elements range from tracheids to libriform fibers. With ranges of character states of this sort, one cannot use wood anatomy to assign families decisively to one order or another.

FAMILIES OF UNCERTAIN POSITION

Apiaceae are included in Table 1 for comparison to sympetalous families. Araliaceae, closely related to Apiaceae, might more logically have been used for comparison, because they contain more woody species. Apiaceae were chosen in preference, however, because Araliaceae contain some species with more primitive character states than Apiaceae. Apiaceae are thus on a similar evolutionary level to more of the sympetalous families. In fact, the wood anatomy of Apiaceae may be indistinguishable from that of Asteraceae (Table 1). This similarity may in part be due to habit, for the Araliaceae, more nearly arboreal, modally differ in habit from woody Apiaceae, which are shrubs, much like the majority of woody Asteraceae. The embryological and chemical similarities of Apiaceae and Araliaceae to Asteraceae (polyacetylenes, sesquiterpene lactones), when added to the wood features common to these families, are imposing. Not all of these are likely to be homoplasies. In the Olmstead & Palmer (1992) phylogeny, Apiaceae and Araliaceae fall not far from the line leading to Asteraceae.

Desfontainiaceae are a monogeneric family for which we do not have data in key embryological and chemical categories. Nevertheless, wood anatomy is significant because the wood features of *Desfontainia* are so primitive. Clearly, *Desfontainia* does not belong in Loganiaceae, its most common placement; the data of Mennega (1980) clearly showed how different Loganiaceae are. Considering that Desfontainiaceae have a preponderance of primitive wood features, one might consider families with similar wood as possible relatives. In

this regard, Columelliaceae are worthy of consideration, as are a number of Escalloniaceae.

Fouquieriaceae have been difficult to place systematically. Most systems have ranked this family close to Cistaceae, Frankeniaceae, or Tamaricaceae. However, Polemoniaceae have been mentioned by a few authors (e.g., Thorne, 1976) as possibly related to Fouquieriaceae. Because Fouquieriaceae contain iridoids, Dahlgren et al. (1976) placed the family in an order of its own near Cornales and Ericales. A feature of Fouquieriaceae not found in Cornales and Ericales (or, for that matter, Polemoniaceae) is the occurrence of two integuments on ovules. With respect to wood anatomy, two features of Fouquieriaceae are rather primitive: presence of tracheids, and presence of diffuse axial parenchyma. Rays of Fouquieriaceae are wide and of a rather specialized type (Homogeneous Type II) not common in sympetalous families. The wood of Fouquieriaceae lacks features to show the familial relationships decisively, and whatever its relatives, the family may be an ancient divergence. Worth mentioning is that the two primitive features cited show that the family has been derived from a phylad with primitive wood. Although Cornales and Ericales are not the only orders with sympetalous families that have notably primitive wood, potential relatives may be found among families that have at least as many primitive wood features as Fouquieriaceae

The small family Salvadoraceae, in which the petals are free or partly united, is known with respect to major embryological features (Table 1). Wood data are also at hand (Metcalfe & Chalk, 1950; Outer & Veenendal, 1981). The occurrence of strands of interxylary phloem within secondary xylem is noteworthy, but this does not appear at present to be a clue to relationships of Salvadoraceae. Neither wood nor embryological features ally Salvadoraceae to Loganiaceae (in which the subfamily Strychneae has interxylary phloem). Storied structure in the wood of Azima of the Salvadoraceae is a distinctive feature. The presence of glucosinolates, not present in any of the sympetalous families, may be a clue that the affinities of Salvadoraceae lie outside of the families considered in the present paper. Salvadoraceae have traditionally been placed in Celastrales because of the supposed presence of a disc. The content of Celastrales has become increasingly uncertain in recent phylogenetic systems of dicotyledons, and Salvadoraceae do not appear to be close to the family Celastraceae. Therefore, Salvadoraceae are currently a good example of a family incertae sedis, much in need of further investigation.

CONCLUSIONS CONCERNING EVOLUTION OF HABIT

Raylessness appears to be an indicator of secondary woodiness: evolution of a moderately woody habit from an herbaceous ancestry is what may be chiefly envisioned, judging from the examples that are available to date. The distribution of raylessness as reported thus far in the sympetalous families is as follows: Acanthaceae: Diapedium, Jacobinia, Thunbergia; Alseuosmiaceae: all genera except Crispiloba; Asteraceae: Lasthenia, Chrysactinia, Dyssodia, Porophyllum, Santolina, Stoebe; Gesneriaceae: Besleria, Cyrtandra; Hydrophyllaceae: Phacelia (one species); Pentaphragmataceae: Pentaphragma; Plantaginaceae: Plantago (all species); Primulaceae: Lysimachia (all species); Polemoniaceae: Cobaea, Leptodactylon; Rubiaceae: Galium; Scrophulariaceae: Calceolaria, Hebe (all species); Selaginaceae: Selago, Walafrida; Stylidiaceae: Stylidium (all woody species).

Another pertinent listing with regard to shift from herbaceous to woody habit is that for taxa in which woods have predominantly upright ray cells. The similarity to raylessness can be seen if one envisions ray cells so tall that they approximate libriform fibers in height. Families in which predominance of upright cells in rays is common, at least in some species, include: Acanthaceae, Asclepiadaceae, Asteraceae, Boraginaceae (a few, e.g., Echium), Calyceraceae, Campanulaceae, Chloanthaceae, Convolvulaceae, Gentianaceae, Gesneriaceae, Goodeniaceae, Hydrophyllaceae, Lamiaceae, Loasaceae, Lobeliaceae, Martyniaceae, Nolanaceae, Pedaliaceae, Plumbaginaceae, Polemoniaceae, Rubiaceae (tribe Rubieae), Scrophulariaceae, Solanaceae (Cestrum, some Solanum species), Stilbaceae, Valerianaceae, Verbenaceae (a few, such as Lantana).

All of the families in both lists or either list are ones in which herbaceous species occur, or are common. Therefore, occurrence of secondary woodiness in at least a few species should not be surprising. Upright ray cells by themselves are not indicative of derivation from an herbaceous ancestry, but only predominance of upright ray cells (preferably combined with other paedomorphic indicators, such as a paedomorphic age-on-length curve in vessel element length: Carlquist, 1962a) indicates secondary woodiness. Thus, some shrubby Asteraceae do not have paedomorphic rays, and this may represent a shrubby ancestry for the family (Carlquist, 1966b). However, most arboreal Asteraceae have a predominance of upright ray cells, thereby indicating that they may be derived from shrubby or even herbaceous ancestors. In a

large and complex family such as Asteraceae, progression from more woody to less woody may have occurred many times independently, and secondary woodiness also may have occurred in many phylads independently. Definitely derived from herbaceous ancestors according to all indicators are such families as Campanulaceae, Lobeliaceae, Plantaginaceae, Pentaphragmataceae, and Valerianaceae. There are instances in which only a small proportion of a family is rayless or has upright ray cells, and thus only one segment of a family may represent secondary woodiness. For example, Rubiaceae are undoubtedly derived from woody ancestors, judged from wood anatomy and the systematic distribution of woodiness in the family. However, *Galium* is an herbaceous genus, with annual species. Species of *Galium* in frost-free climates, such as southern California, are perennial and can develop a moderate amount of wood. Given this limited amount of information, one cannot say that all species of *Galium* are secondarily woody; some might represent a transition between woody ancestors and the annual habit. However, in any particular subgenus of *Galium*, distribution of woodiness with relation to character states of other characters might demonstrate the likelihood of secondary woodiness, as demonstrated by cladistic means.

In this regard, the work of Baldwin (1989) on the subtribe Madiinae, tribe Heliantheae of Asteraceae, is noteworthy. Because the DNA evidence with which Baldwin deals is so readily polarizable, the likelihood of a cladistic hypothesis generated from such data is extremely high. Thus, we can say with great assurance, based on the data of Baldwin et al. (1991), that the Hawaiian Madiinae are derived from a clade of Californian Madiinae, and that the Hawaiian Madiinae are derived from ancestors all of which could be put in the genus *Madia*, if a broad generic concept (including *Raillardella* and *Raillardiopsis*) were considered. A hybrid between *Raillardella* and the Hawaiian genus *Dubautia* has been produced (Baldwin & Kyhos, unpublished). The Californian species of *Madia*, even in an extremely broad concept, are annuals or minimally woody perennials. There is every reason to believe that the extant species are very similar in habit to the immediate ancestors of the Hawaiian Madiinae. Thus, the Hawaiian species of *Dubautia* and *Wilkesia*, which are shrubs or trees, are clearly secondarily woody. Increasingly, it will be possible to use DNA evidence to demonstrate, using cladistic means, the likelihood of secondary woodiness in particular groups.

The data from wood anatomy do, however, give

excellent circumstantial evidence that phylesis toward herbaceousness is common in the sympetalous families, and that in a number of phylads (very likely the rayless ones plus many of the phylads with predominantly upright ray cells) secondary woodiness has occurred. Compared with dicotyledons at large, trends to or from herbaceousness in the sympetalous families seem relatively common.

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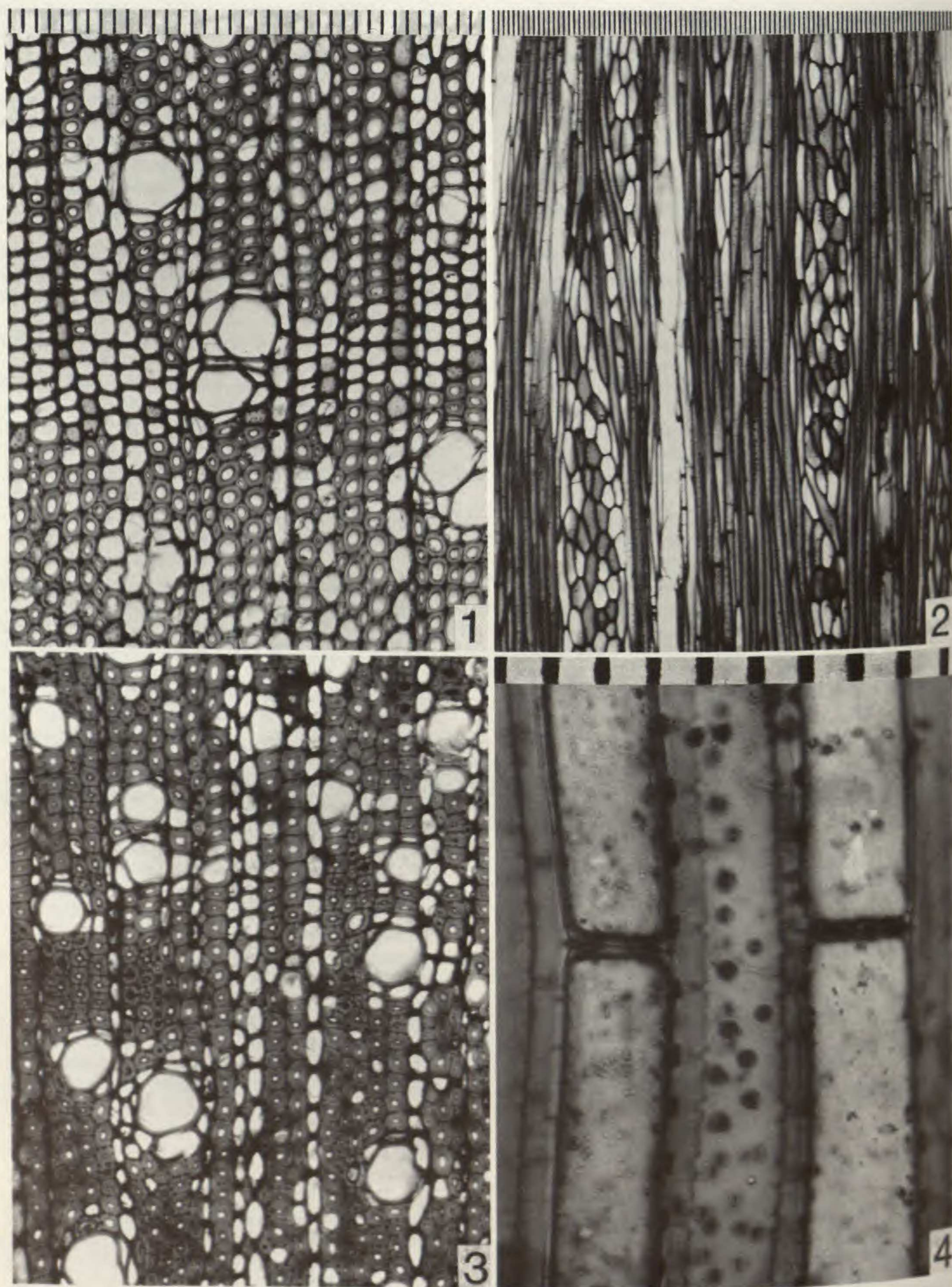
FIGURES 1–4.   Wood sections of *Coprosma* (Rubiaceae). 1, 2. *C. montana* (*USw-15336*).—1. Transection; band of axial parenchyma near middle.—2. Tangential section; rays are multiseriate, composed mostly of upright cells. 3, 4. *C. foliosa* (*USW-15307*).—3. Transection; axial parenchyma is scanty vasicentric plus a few diffuse cells.— 4. Tracheid (center) with axial parenchyma on either side, from radial section; pits on tracheid are small but fully bordered. Figures 1, 3, magnification scale above Figure 1 (divisions = 10 μm). Figure 2, scale above Figure 2 (divisions = 10 μm). Figure 4, scale above Figure 4 (divisions = 10 μm).
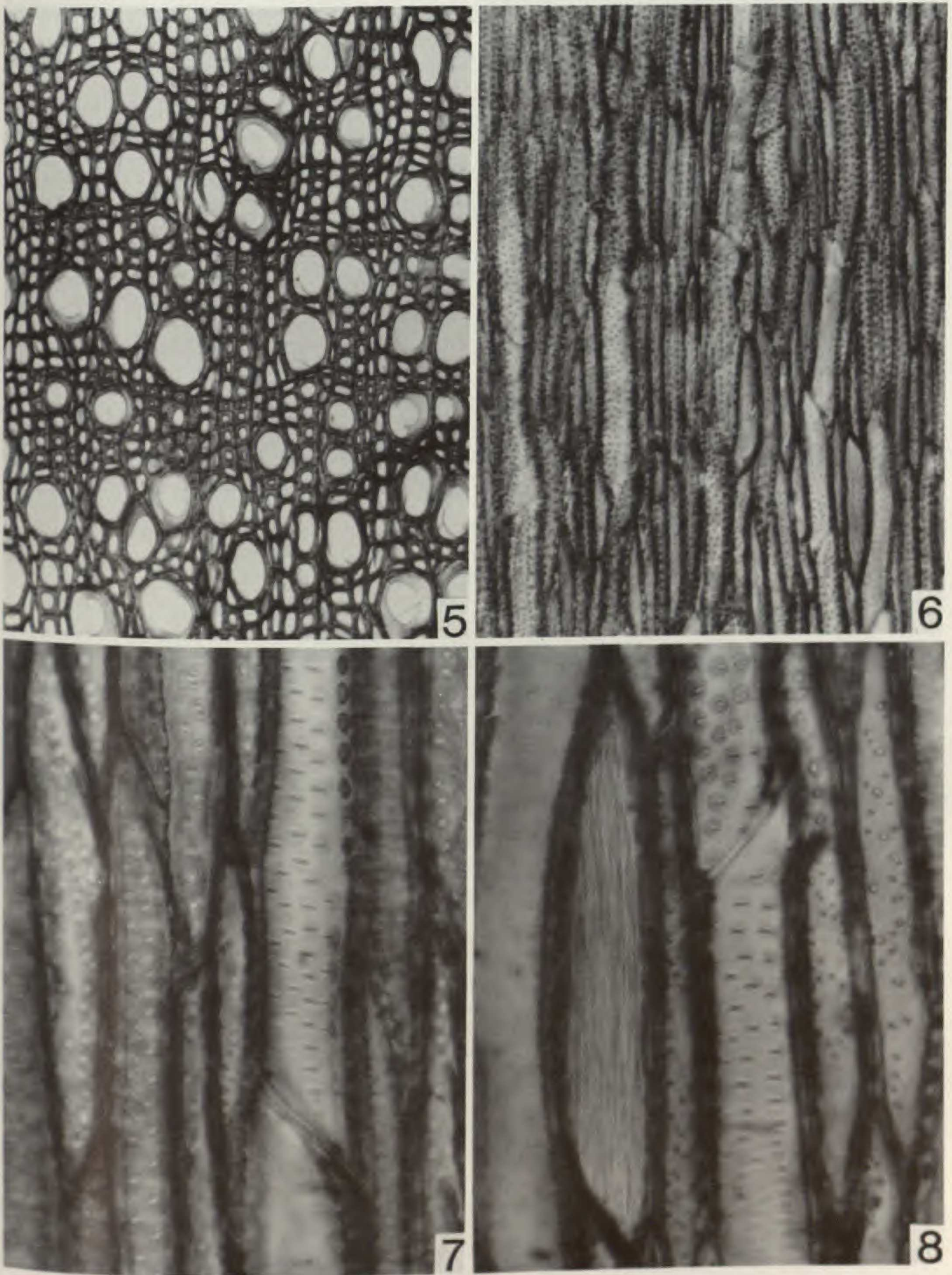
FIGURES 5–8. Wood sections of *Galium catalinense* (*Davidson 1517*, RSA).—5. Transection; vessels are mostly solitary.—6. Tangential section, showing nearly rayless condition; storying is present.—7. Portion of tangential section, to show vessel and tracheids with small but fully bordered pits.—8. Portion of tangential section; vessel, parenchyma cells at right, ray cell containing raphides at left. Figures 5, 6, scale above Figure 1. Figures 7, 8, scale above Figure 4.
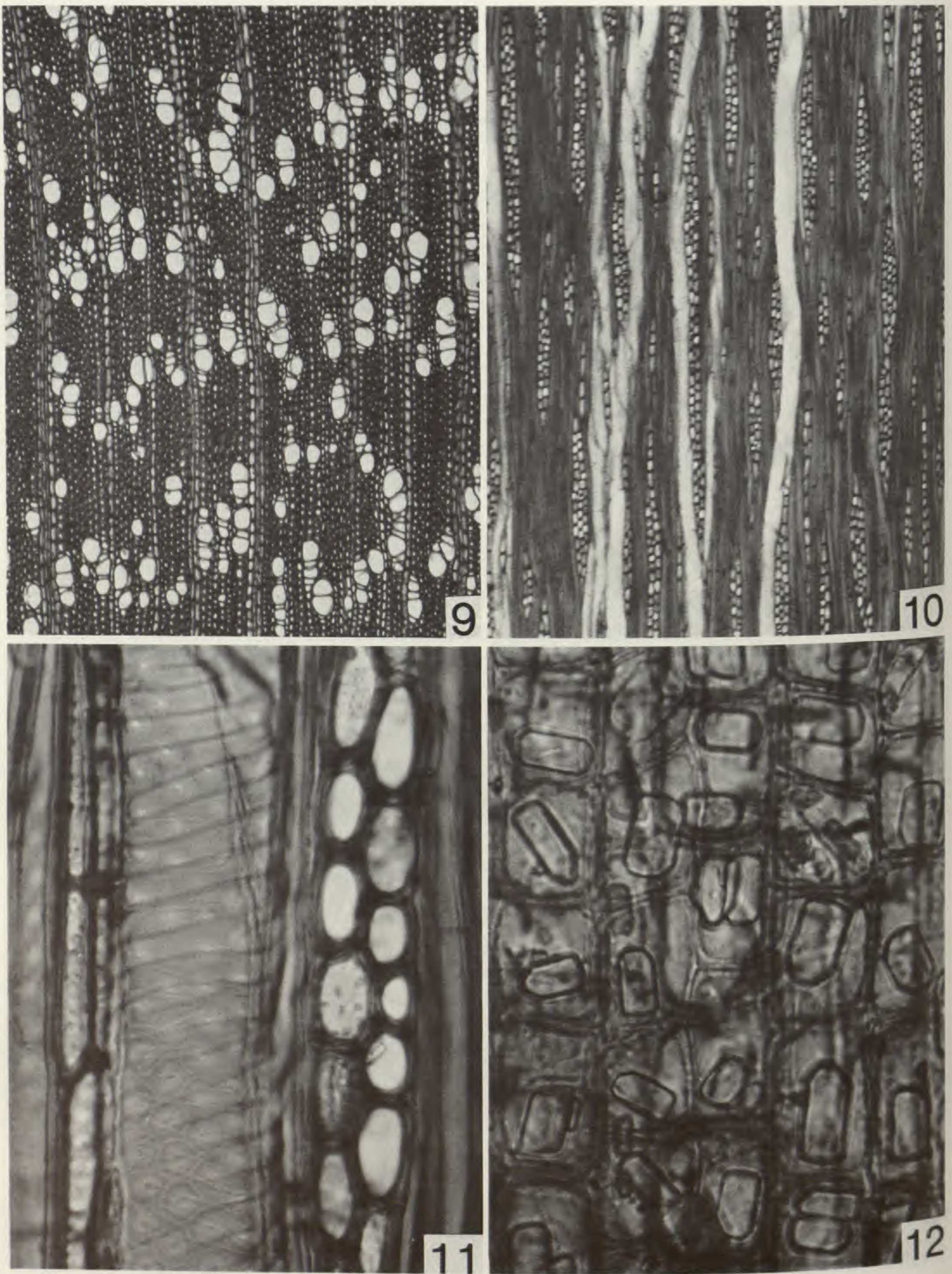
FIGURES 9–12. Wood sections of *Buddleja globosa* (*Carlquist 7278*, RSA).—9. Transection; vessels are not in large groupings.—10. Tangential section; uniseriate rays are about as frequent as multiseriate rays.—11. Vessel and portion of ray from tangential section; helical thickenings present in vessel.—12. Ray from radial section (horizontal axis of ray oriented vertically) to show crystals in ray cells. Figures 9, 10, scale above Figure 2. Figures 11, 12, scale above Figure 4.
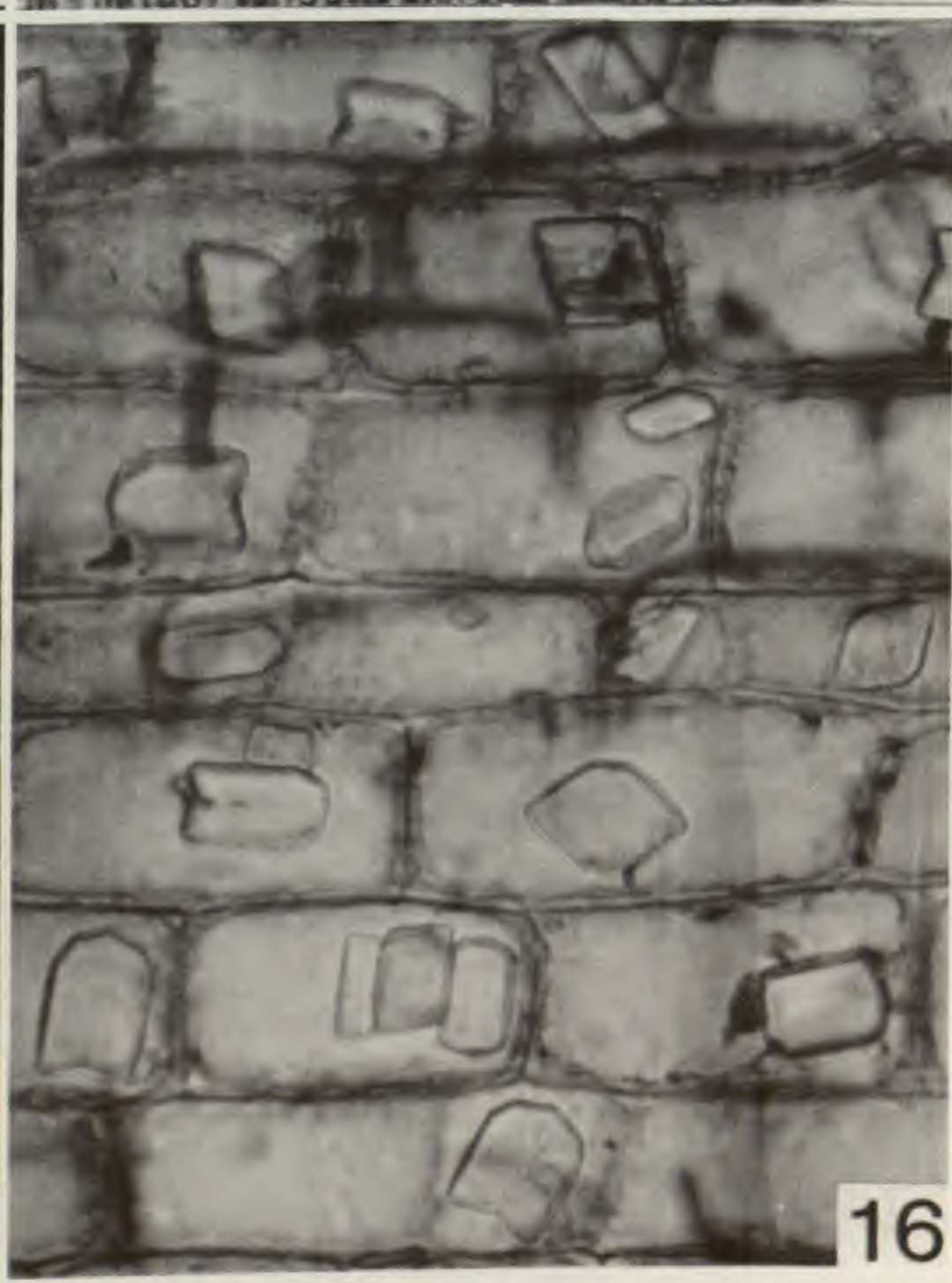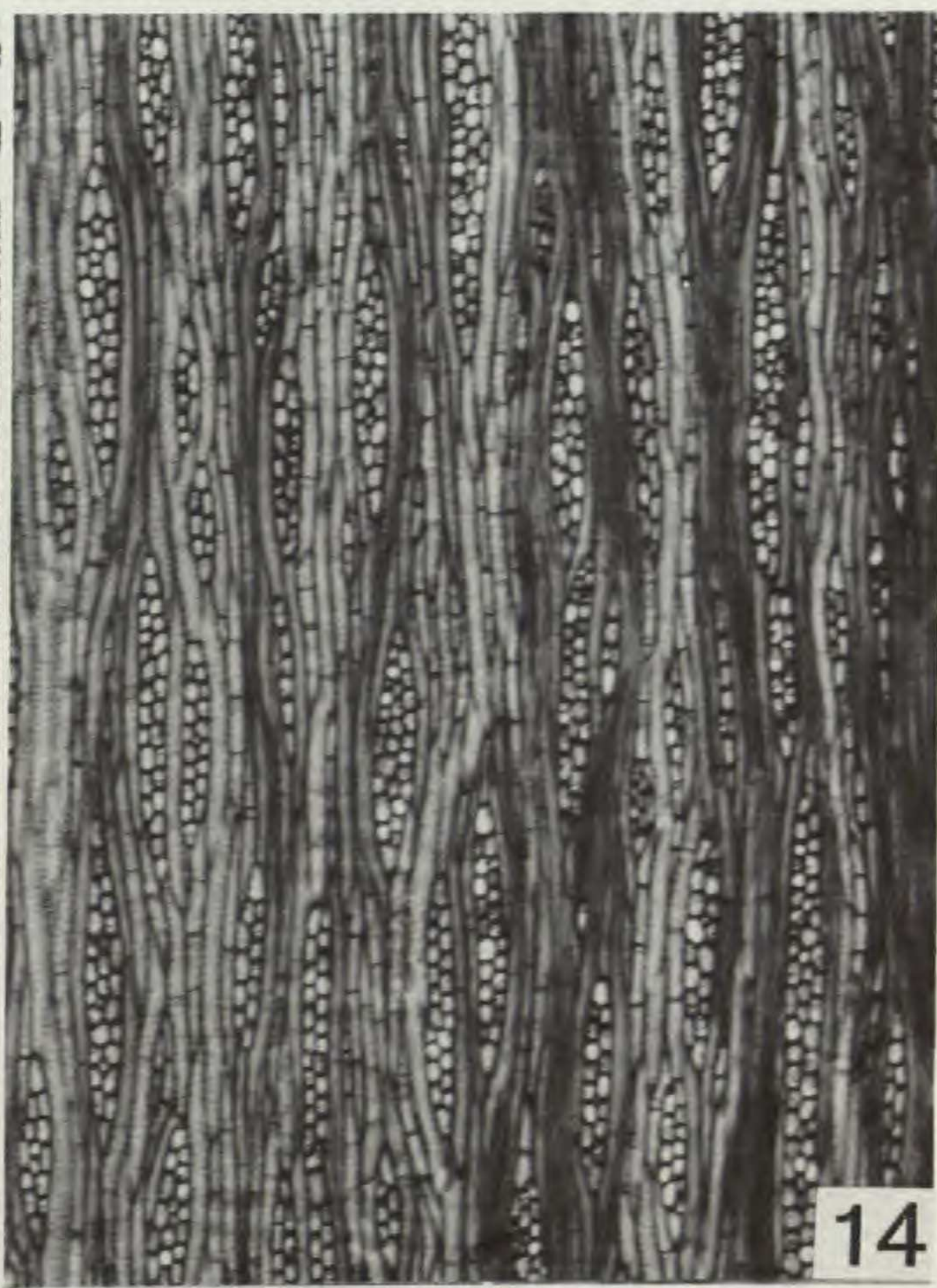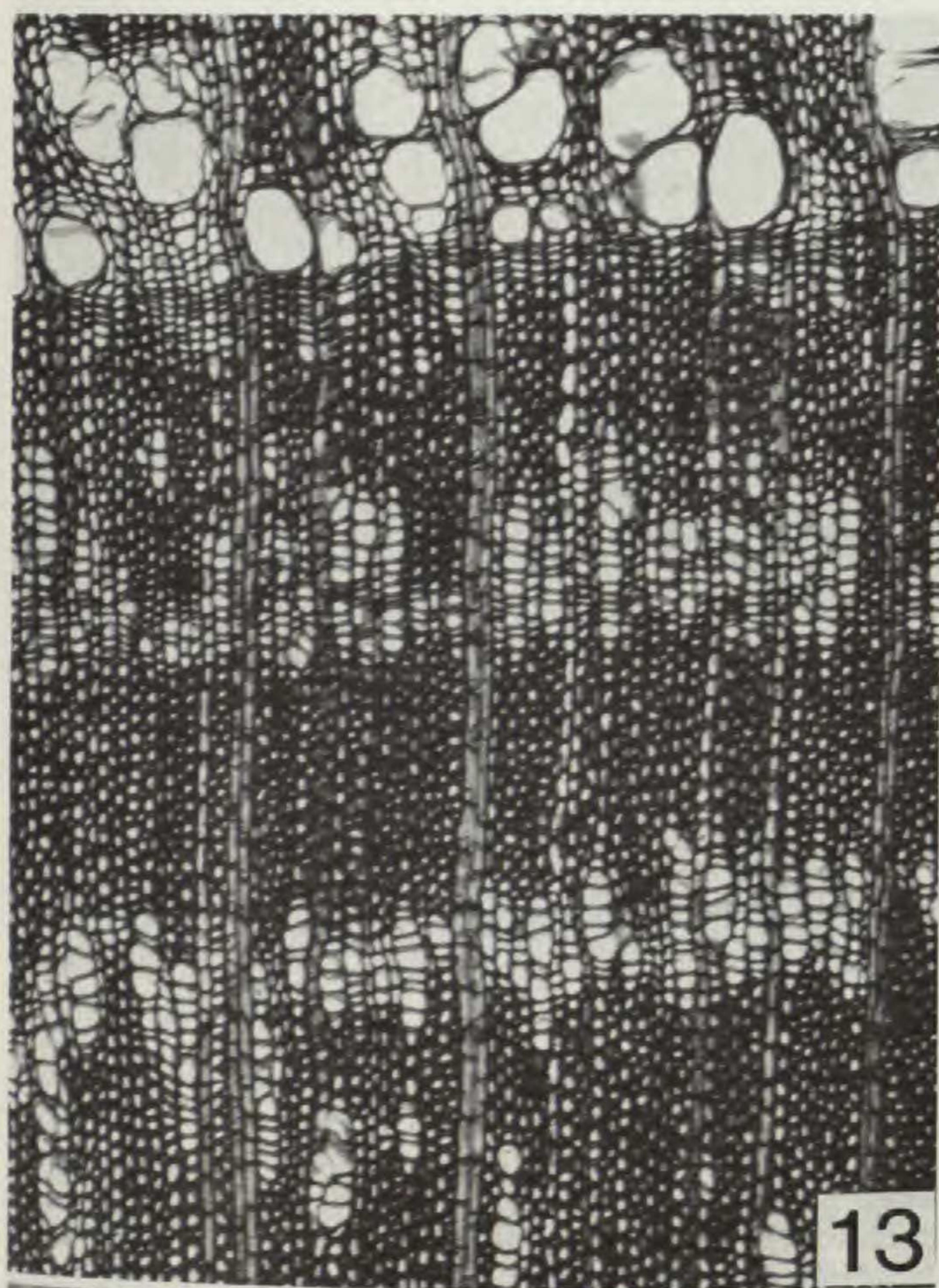
FIGURES 13–16.   Wood sections of *Buddleja parviflora* (*Iltis & Koeppen 106*, MAD).—13. Transection, showing earlywood at top; most of photograph is latewood, which contains tangential bands of narrow vessels.—14. Tangential section; uniseriate rays are infrequent.—15. Latewood vessels from radial section, showing helical thickenings.—16. Ray cells from radial section to show types of crystals present. Figures 13, 14, scale above Figure 2. Figures 15, 16, scale above Figure 4.
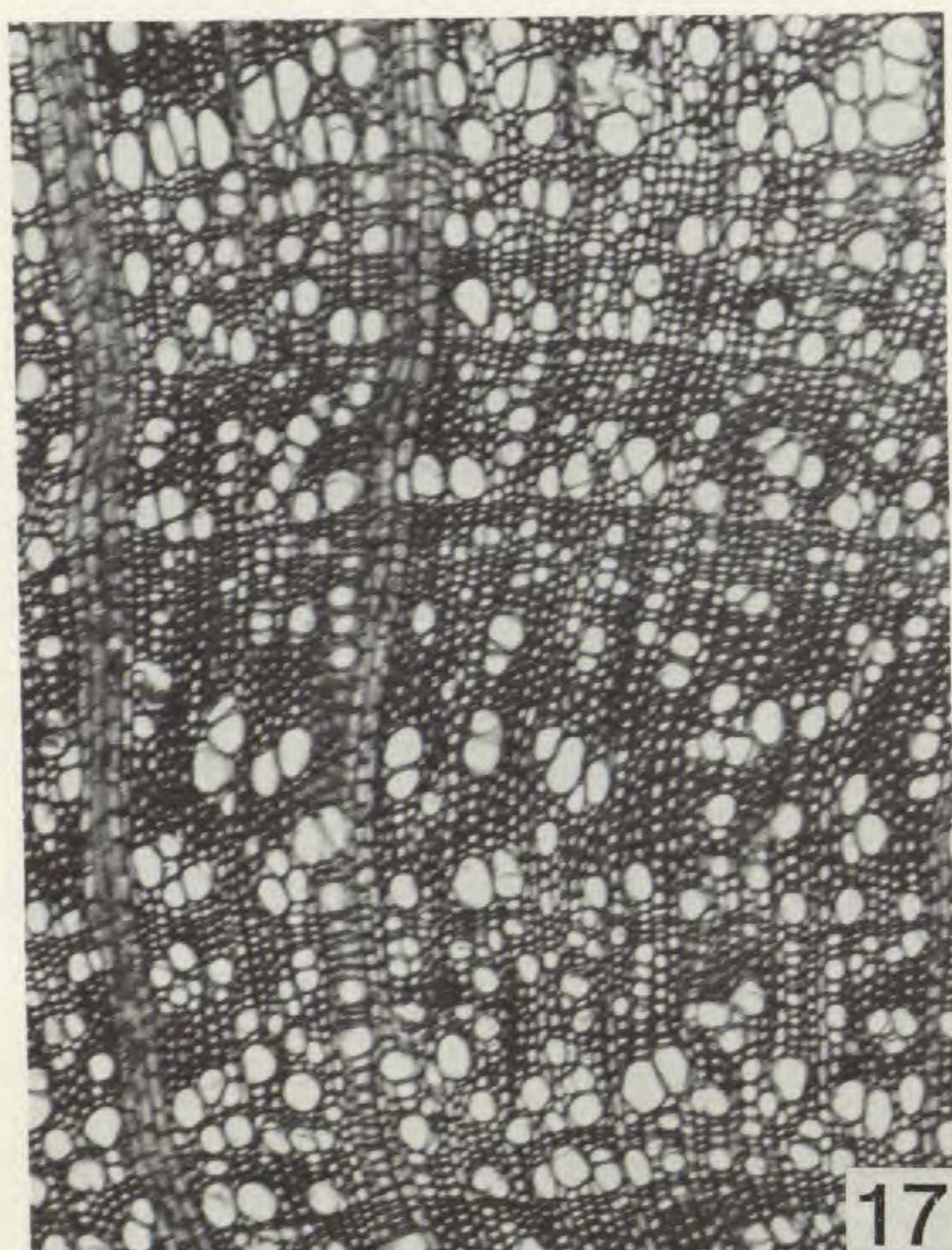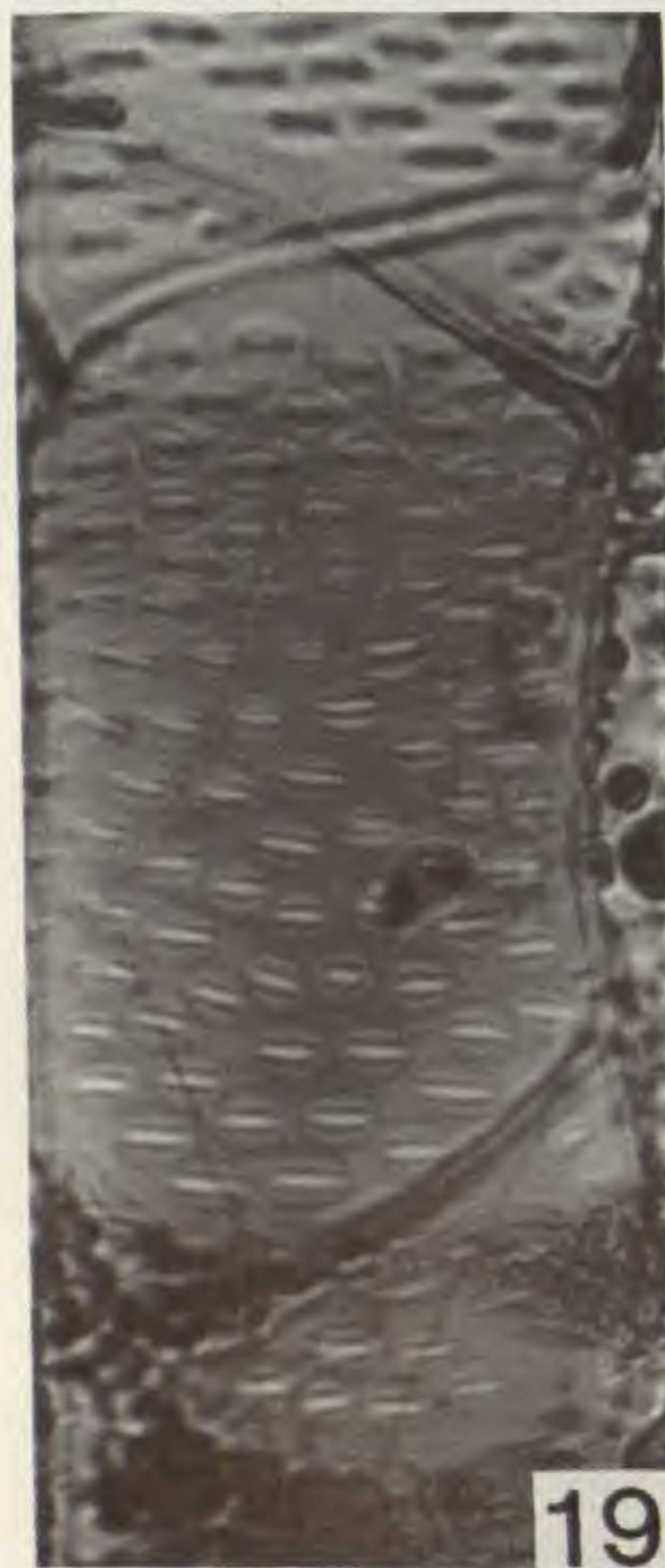
FIGURES 17–21.   Wood sections of *Buddleja utahensis* (*Thorne 44537*, RSA).—17. Transection, showing several weakly defined growth rings.—18. Tangential section; rays are few but wide.—19. Vessel from earlywood; helical thickenings are absent.—20. Vessel and (left) vasicentric tracheid from latewood; helical thickenings are present.— 21. Ray cells from radial section (horizontal axis of ray oriented vertically) to show elongate crystals. Figures 17, 18, scale above Figure 2. Figures 19–21, scale above Figure 4.
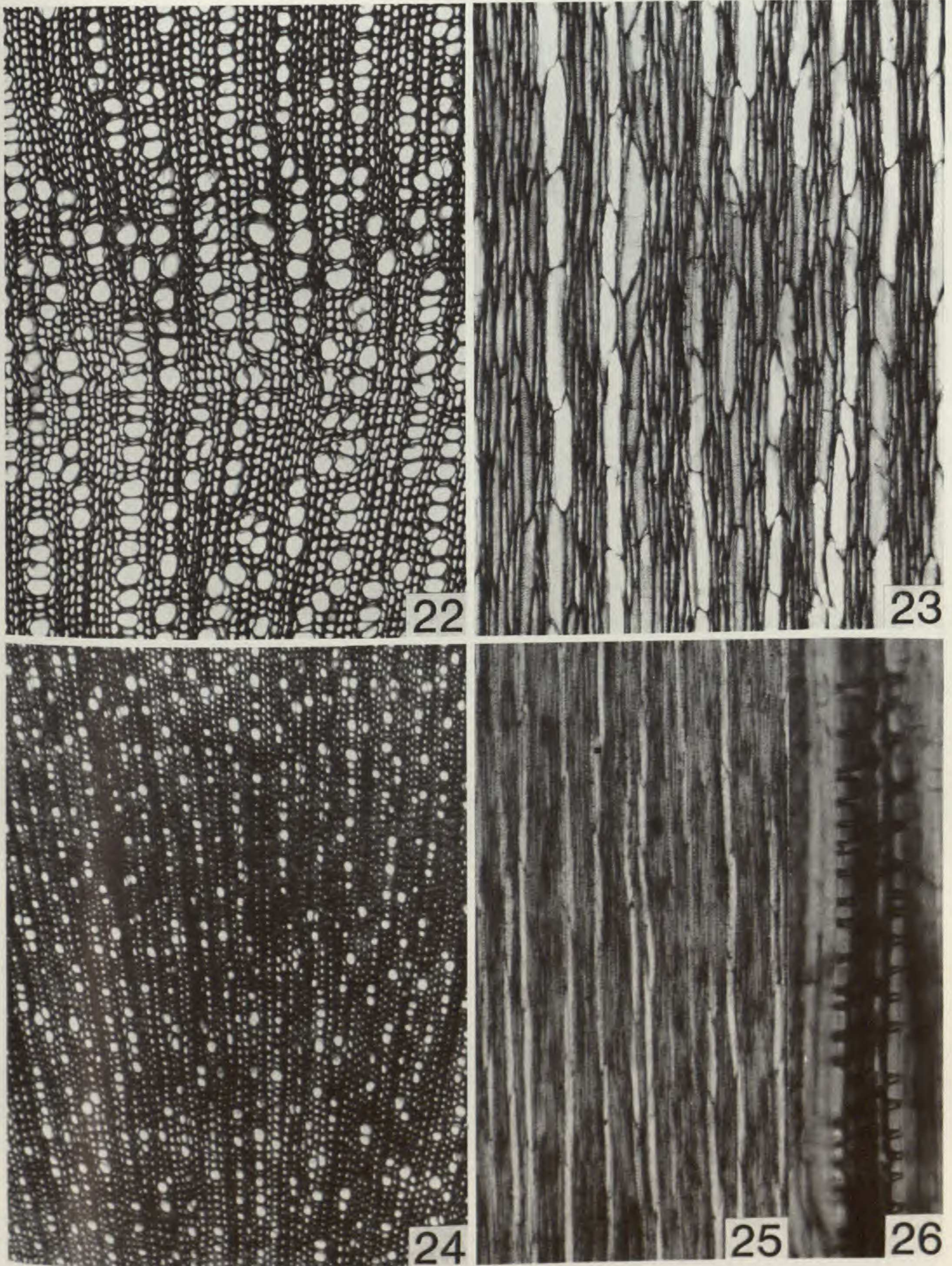
FIGURES 22–26. Wood sections of rayless Scrophulariaceae. 22, 23. *Calceolaria adscendens (Carlquist 7224,* RSA).—22. Transection; vessels are in radial chains and radial multiples.—23. Tangential section to show raylessness; some storying is present. 24–26. *Hebe elliptica (Carlquist 8151,* RSA).—24. Transection; vessels are very narrow and mostly solitary.—25. Tangential section to show rayless condition.—26. Fiber-tracheid from tangential section; air in the fiber-tracheid outlines the pits, which have vestigial borders. Figures 22–25, scale above Figure 2. Figure 26, scale above Figure 4.
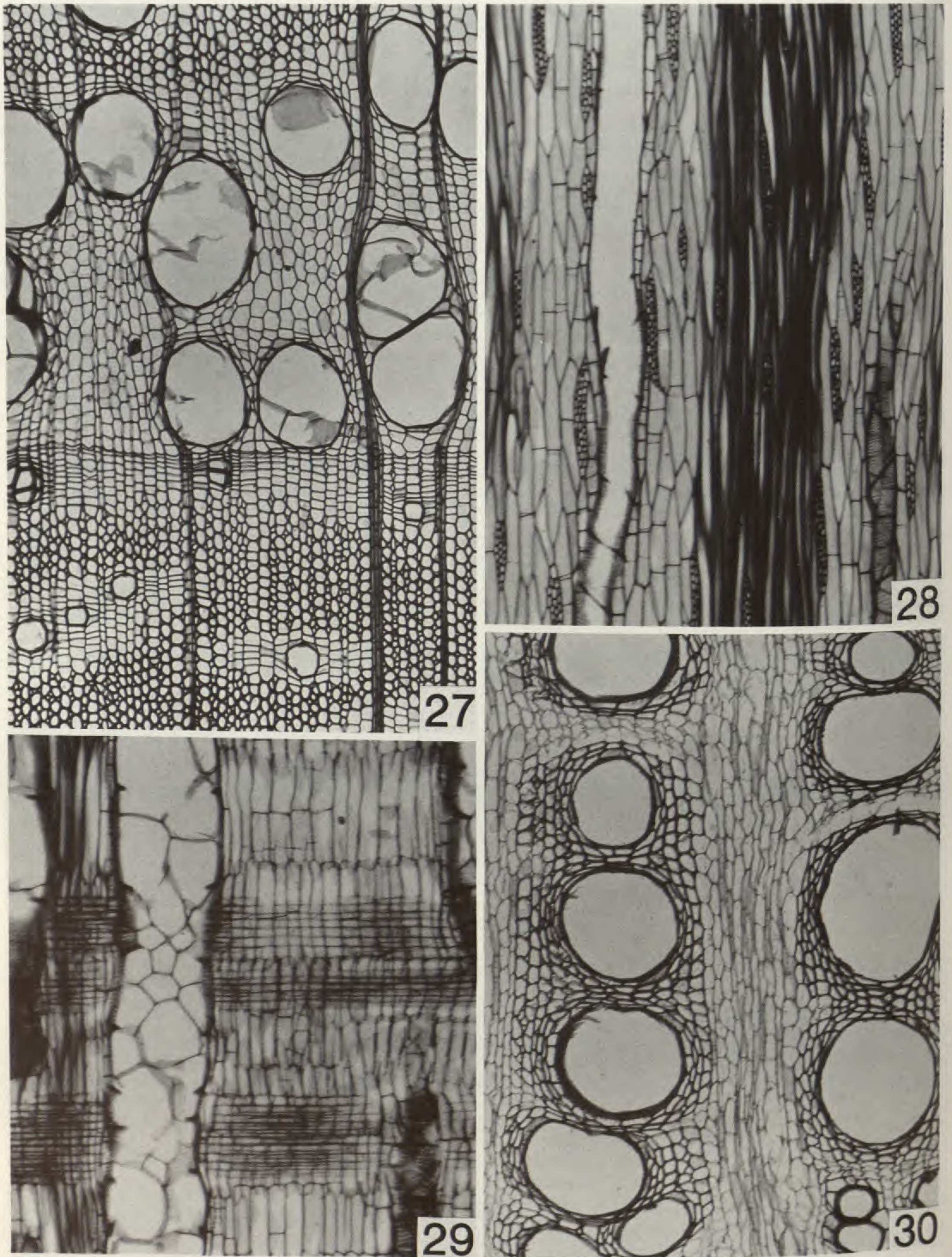
FIGURES 27–30. Wood sections of *Paulownia* and *Faradaya*. 27–29. *Paulownia tomentosa* (no collection data).—27. Transection; extensive axial parenchyma in earlywood (above); aliform axial parenchyma in latewood (below).—28. Tangential section (dark cells, center, are libriform fibers); rays are Homogeneous Type II.—29. Radial section; axial parenchyma cells undivided or in strands of two cells; tyloses in vessels, right.—30. *Faradaya splendens* (SFCw-R1185-110), transection; the vessels are wide, sheathed by libriform fibers. Figures 27–29, scale above Figure 2.
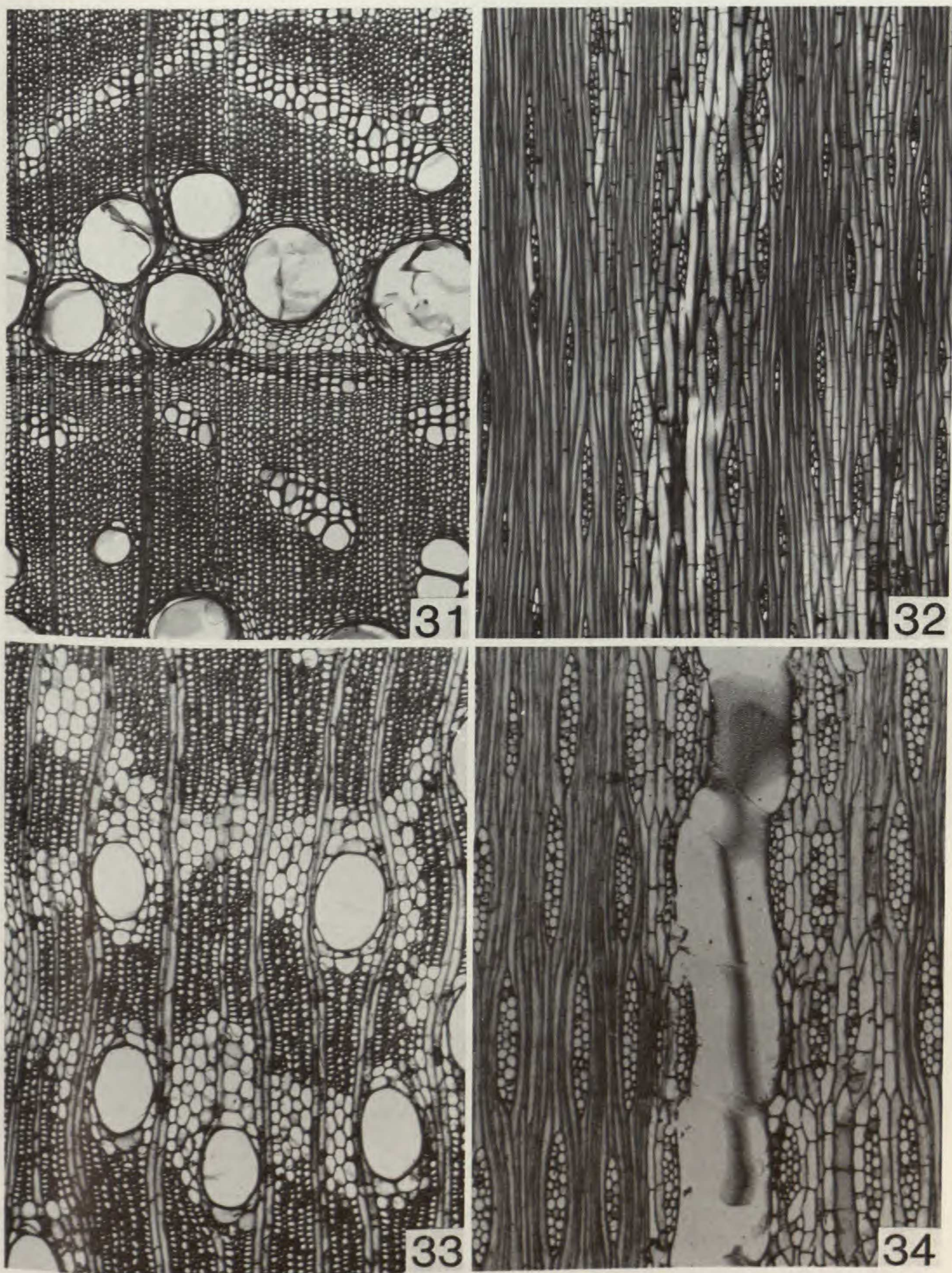
FIGURES 31–34. Wood sections of Bignoniaceae. 31, 32. *Catalpa speciosa* Warder (no collection data).—31. Transection; extensive axial parenchyma in earlywood (just above center); axial parenchyma is scanty vasicentric in latewood (top, latewood vessels are in diagonal aggregations).—32. Tangential section; rays are not storied. 33, 34. *Tecoma pentaphylla* (USw-5600).—33. Transection; axial parenchyma is aliform-confluent.—34. Tangential section; rays are storied. Figures 31–34, scale above Figure 2.
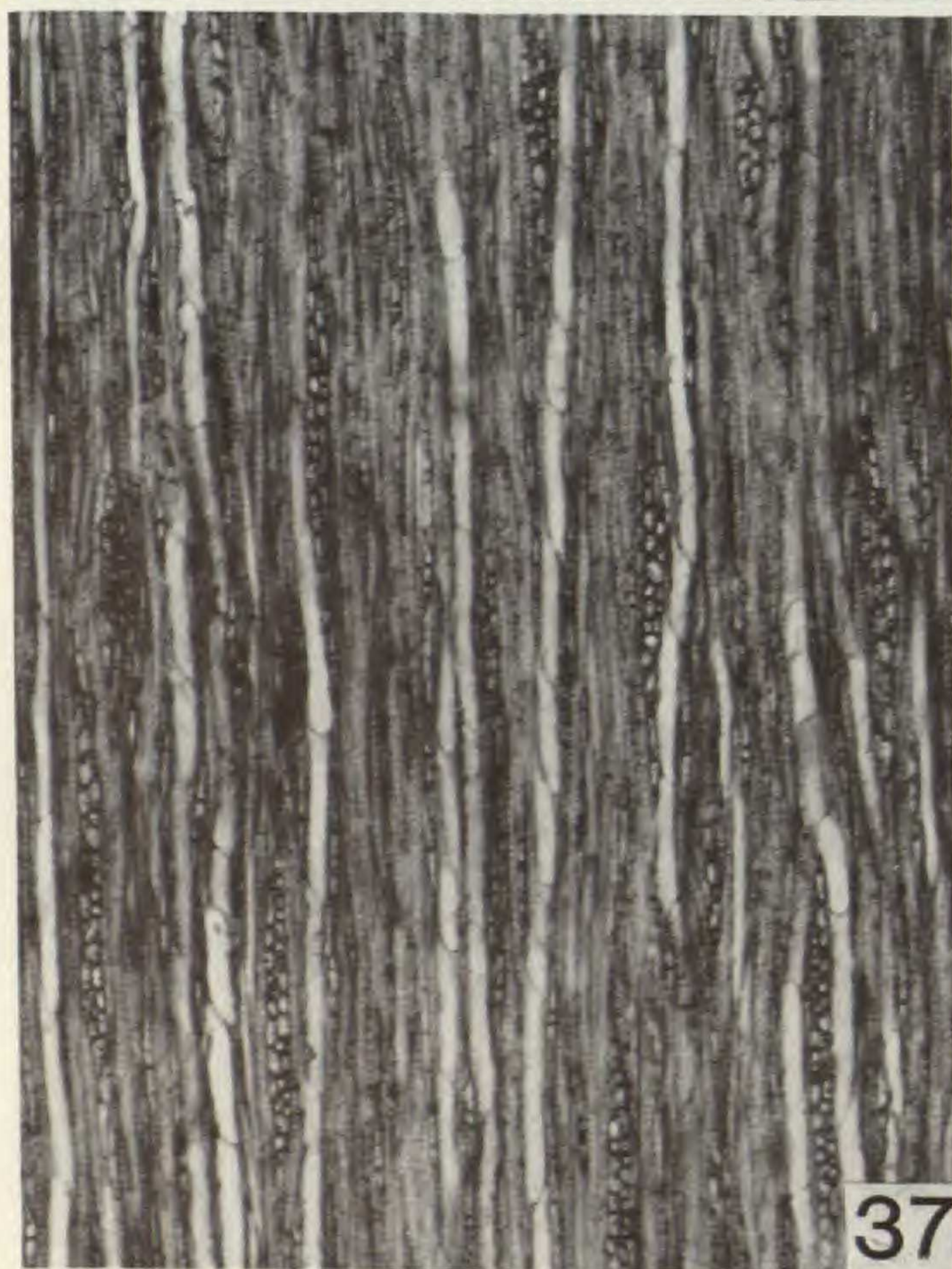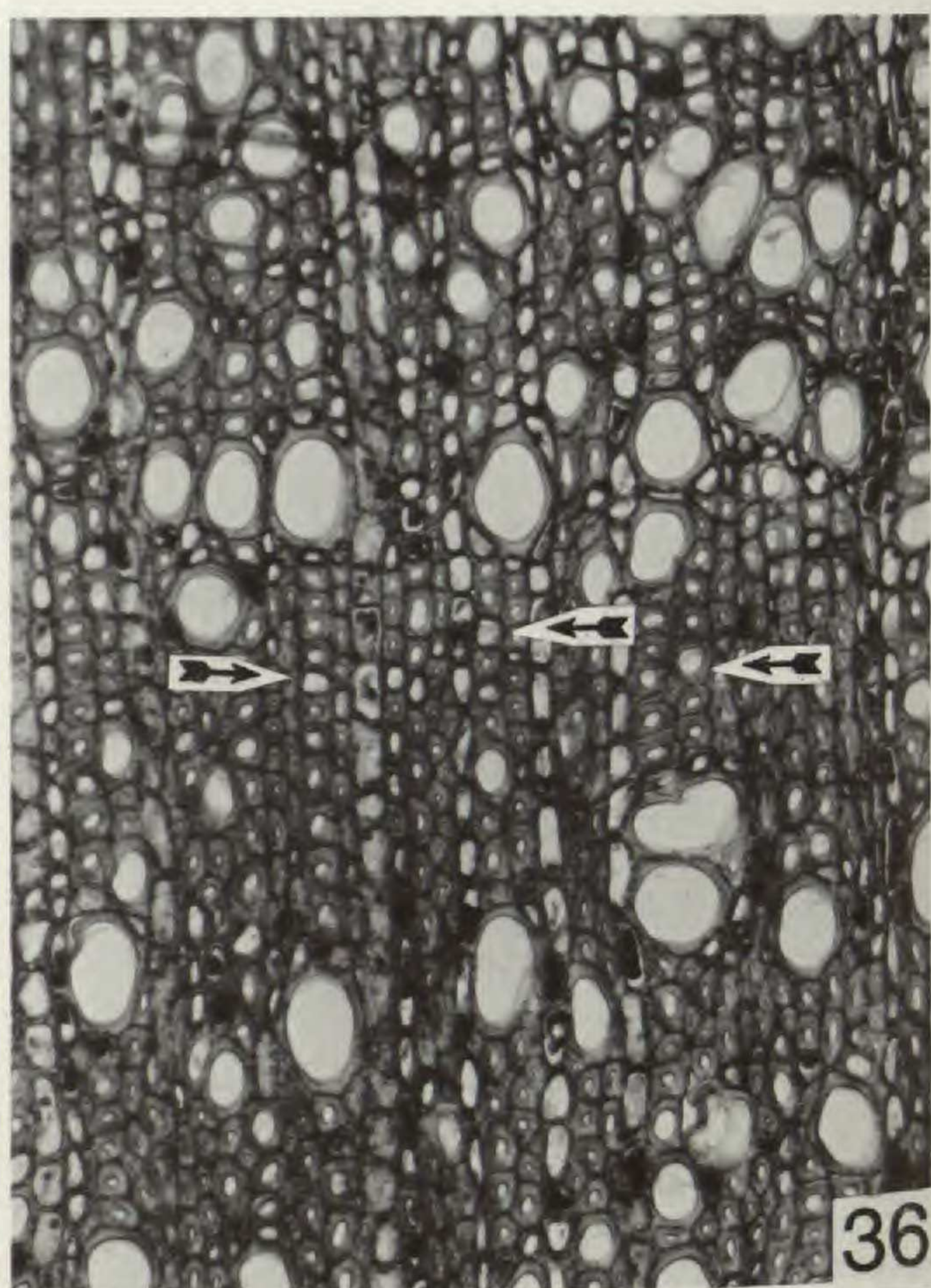
FIGURES 35–38.   Wood sections of *Globularia salicina* (*Carlquist 2629*, RSA).— 35. Transections; vessels are mostly solitary.— 36. Portion of transection; axial parenchyma is diffuse (two such cells are indicated with arrows) and scanty vasicentric.— 37. Tangential section; rays are Heterogeneous Type IIA.— 38. Portion of tangential section to show numerous bordered pits in tracheids. Figures 35, 37, scale above Figure 2. Figure 35, scale above Figure 1. Figure 38, scale above Figure 4.
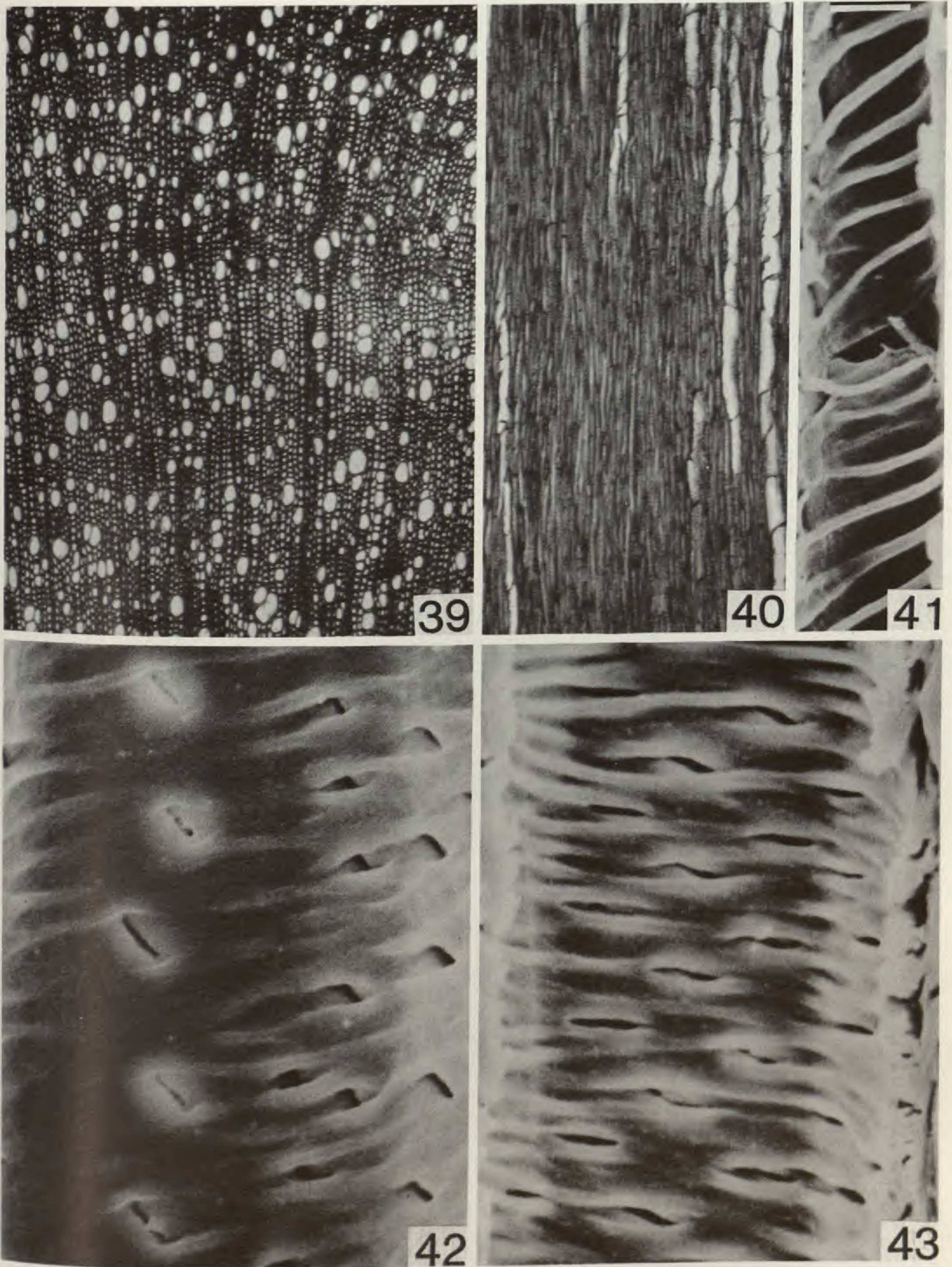
FIGURES 39–43. Wood sections of Selaginaceae. 39, 40, 43. *Walafrida nitida (Carlquist 8062)*.—39. Transection; growth rings are absent.—40. Tangential section; rays are absent. 41, 42. *Selago thunbergii (Carlquist 8061)*, SEM photographs from tangential sections.—41.Vasicentric tracheid; helical thickenings are prominent.—42. Wide vessel wall; helical thickenings are present but not pronounced.—43. SEM photograph of vessel from tangential section to show helical thickenings. Figures 39, 40, scale above Figure 2. Figures 41–43, bar at top of Figure 41 (bar = 1 μm).
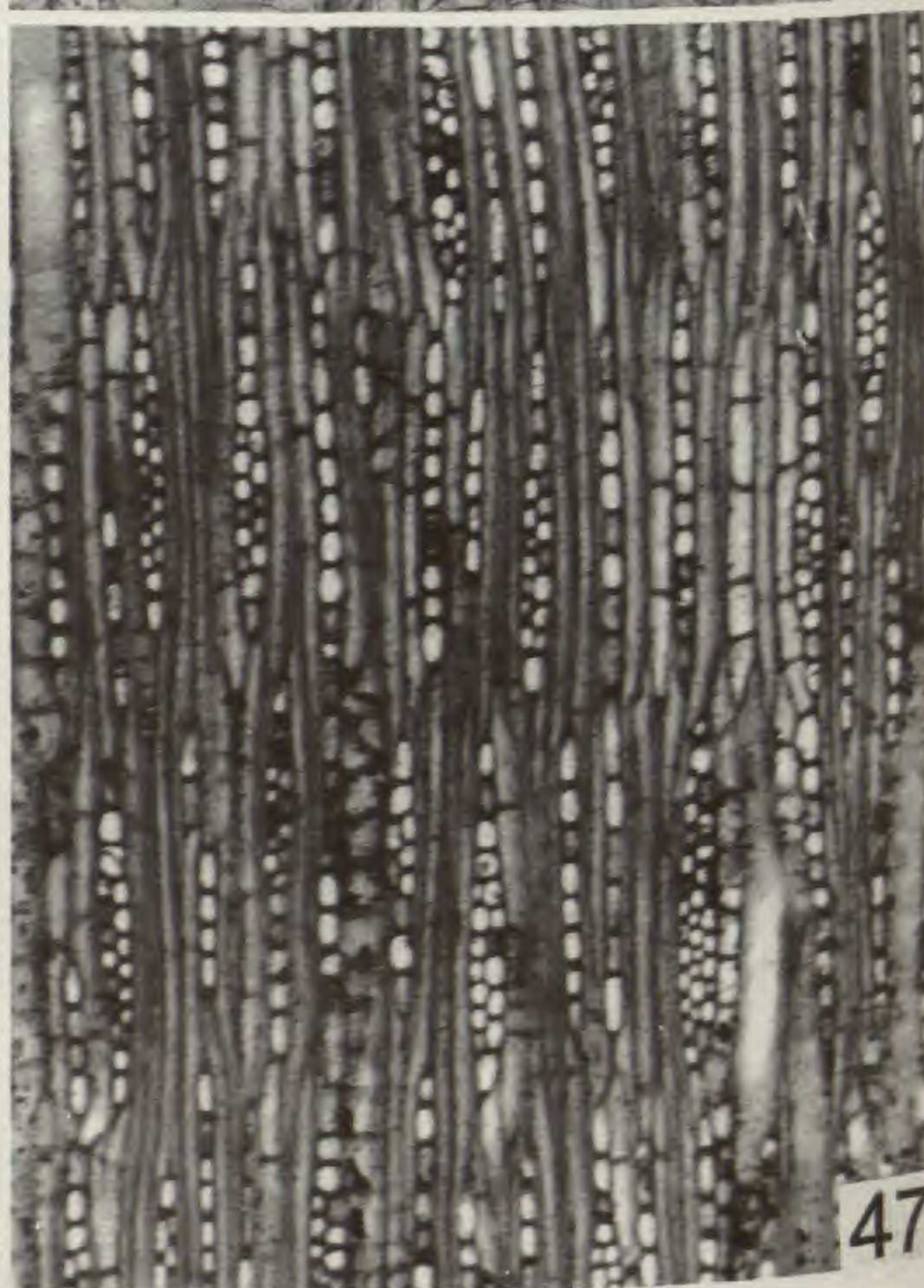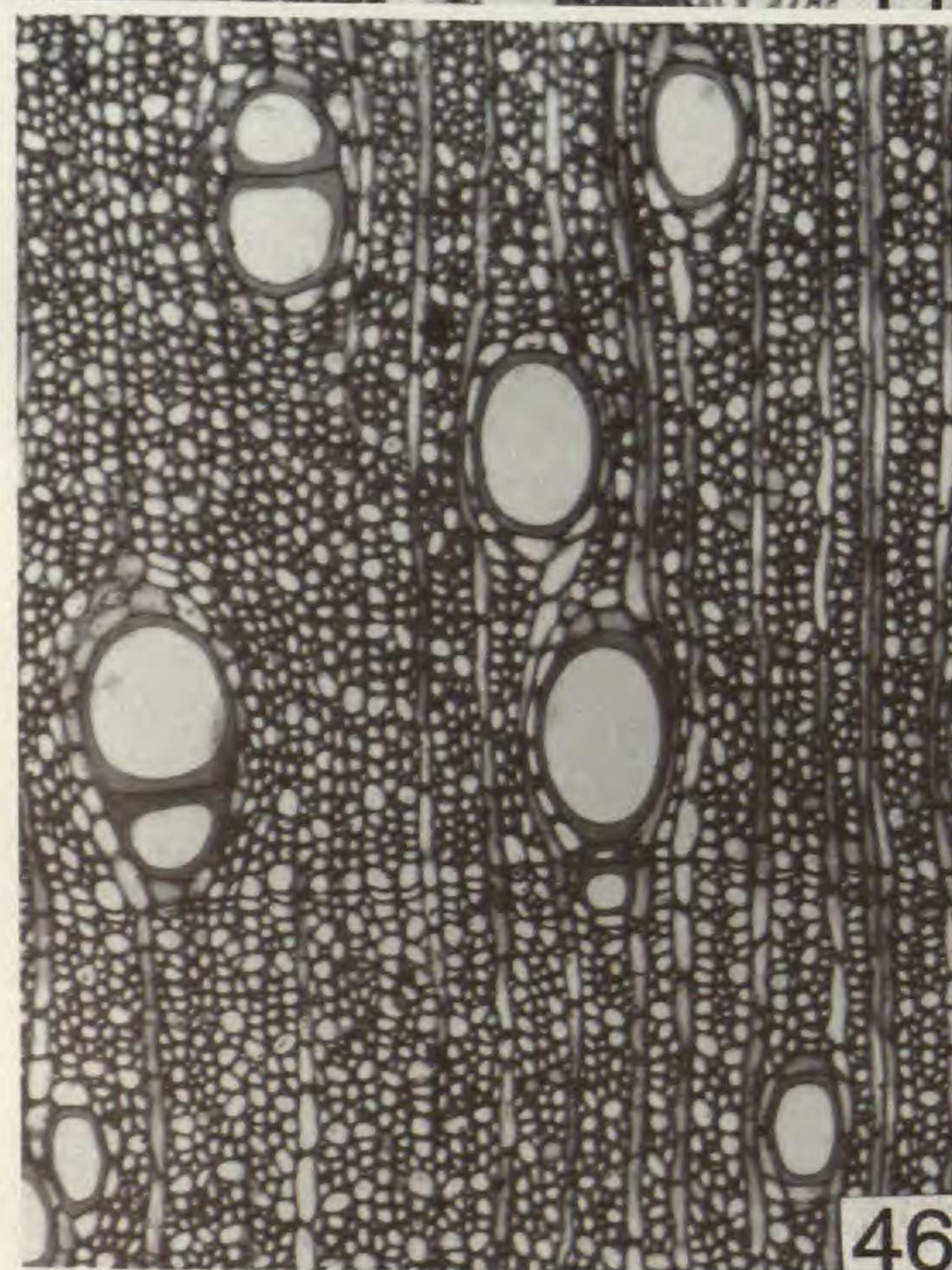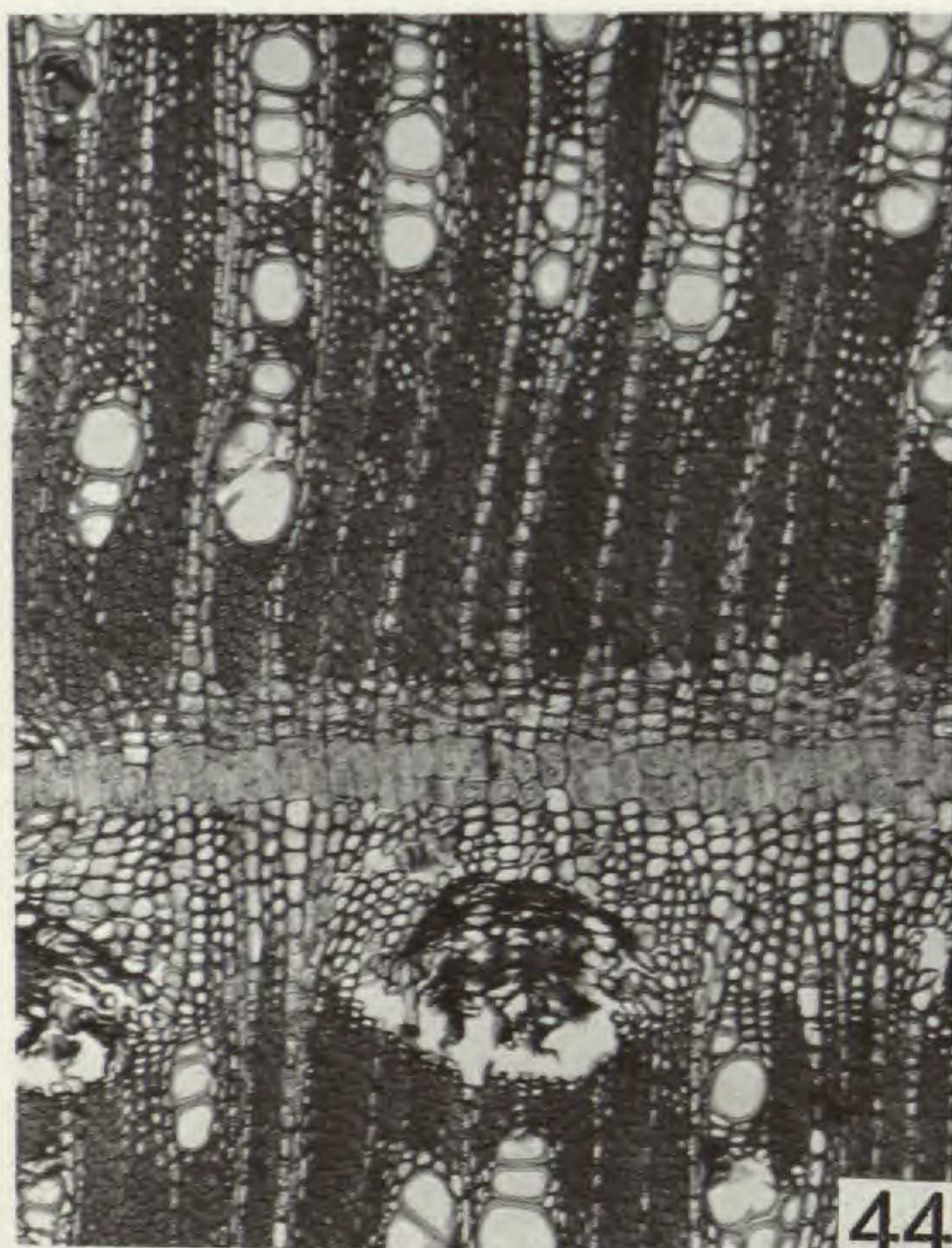
FIGURES 44–47. Wood sections of Avicenniaceae and Ebenaceae. 44, 45. *Avicennia marina* Vierh. (*USw-4255*).—44. Transection; conjunctive tissue, just below center, contains a sclerenchyma band.—45. Radial section, showing crystals in conjunctive tissue cells; sclerenchyma band, left. 46, 47. *Diospyros virginiana* L. (*US2-20364*).—46. Transection; axial parenchyma is diffuse, diffuse-in-aggregates, vasicentric.—47. Tangential section; rays are storied. Figures 44–47, scale above Figure 2.